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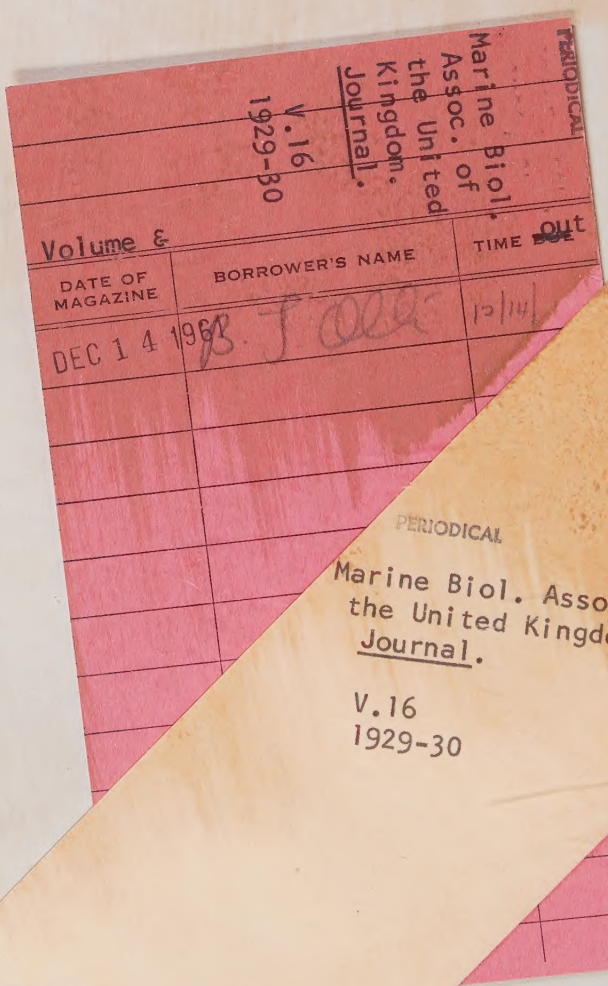

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Herring Investigations at Plymouth. V. The Plymouth Winter Fishery during the Season 1927–28.

By

E. Ford, A.R.C.Sc.,

Naturalist at the Plymouth Laboratory.

With 7 Figures in the Text.

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During the winter of 1927–28 the progress of the herring fishing at Plymouth was followed for the fourth consecutive season. A diary of market events was again kept by Mr. A. J. Smith of the Laboratory staff, while statistics of commercial landings and of the number of visiting drifters were kindly supplied by Mr. T. Edser of the Statistical Department, Ministry of Agriculture and Fisheries, and by Mr. E. C. Nelder of the Sutton Harbour Improvement Company, respectively. In the examination of age and growth of random samples of herrings, Mr. F. J. Warren, Laboratory Assistant, again acted as recorder. Details of the methods of treatment of the data collected will be found in Part I of this series of Reports (Ford, **1**).

The Winter Fishery of 1927–28.

The season was in several ways a notable one. It will be seen from the following table that in spite of a marked reduction in the number of

boats fishing, particularly in the case of steamers, the total quantity of herrings landed created a record :—

Season Dec.-Jan.	Number of East Country steamers.	Number of West Country (Cornish) motor drifters*	Total Quantity of Herrings landed. cwt.	Quantity landed by steamers only. cwt.	Quantity landed by motor drifters† only. cwt.
1918–19	33	139	8,624	7,628	996
1919–20	30	156	29,425	12,728	16,697
1920–21	26	182	40,263	20,973	19,290
1921–22	31	155	16,922	10,494	6,428
1922–23	68	142	54,839	40,941	13,898
1923–24	59	161	98,684	57,519	41,165
1924–25	86	176	113,585	83,647	29,938
1925–26	153	158	105,643	82,780	22,863
1926–27	129	169	63,138	45,932	17,206
1927–28	77	145	122,419	82,803	39,616

The Steam Fishery.

There has been an appreciable decline in the number of steamers visiting Plymouth during the past two seasons, due, probably, to the fact that the fishery had experienced several indifferent seasons in succession. In the months of December, 1927, and January, 1928, however, the seventy-seven steamers made a total of 1789 landings of an average weight of 46·6 cwt. This result was a welcome improvement on the averages for the corresponding months of the seasons 1925–26 and 1926–27 (23·1 cwt. and 16·6 cwt. respectively), as well as on the average of 26·6 cwt., covering the longer period of nine seasons from December, 1918, to January, 1927.

Whether or no the steamers, by ceasing fishing towards the end of January, leave the district when fishing might yet prove profitable, is a question worthy of investigation. The work of the past few years has created the impression that to the westward of Plymouth there may be an assemblage of well-grown, comparatively later-spawning herrings which are not every year fully exploited. Some of the small local drifters, when weather permits, certainly continue to make catches until well on into March, while the study of fishes landed during February and March has shown that an appreciable proportion of them have yet to spawn. Wallace (**4**, p. 35), too, has shown that later spawning of considerable intensity does occur in westerly waters in the neighbourhood of Gribbon Head. In such a season as the one now under review, when consistently good catches to the eastward are made, there is a decided tendency to bring the fishery to a close as soon as the easterly shoals show signs of exhaustion. In consequence of this, the late westerly fish are liable to be almost entirely neglected.

* A small number of Plymouth motor drifters take part in the fishery, numbering on average about twelve.

† These figures are inclusive of the landings by Plymouth boats.

The Motor Fishery.

The total weight of fish landed by the motor drifters during December, 1927, and January, 1928, was the heaviest since the record season of 1923–24. This satisfactory aggregate, however, in contrast with that of the steamers, was chiefly due to a considerable rise in the total number of landings made, rather than to an increase in the average weight per individual landing. Thus, although the total number of landings was the greatest recorded since the Ministry's more modern system of statistics was adopted in 1906, the average weight of 24·6 cwt. per landing did not greatly exceed the average of 22·6 cwt. for the nine-year period from December, 1918, to January, 1927.

As in past seasons, a considerable weight of fish was landed by the steamers on days when the motor drifters made no landings. Thus, on 22 days (inclusive of 6 Sundays) during December, 1927, and January, 1928, a total of 29,708 cwt. was landed by steamers, while there were no landings at all by motors.

Value of the Fishery.

The total value of the fishery during each of the past twenty-two seasons is shown in the following table, together with the average price per 1 cwt. : –

Season (Dec.–Jan.)	Total Weight landed. (cwt.)	Total Value. £	Average Price per 1 cwt. shillings and pence.
1906–07	32,913	8,040	4 11
1907–08	23,957	6,583	5 6
1908–09	4,257	2,521	11 10
1909–10	52,544	16,105	6 1
1910–11	37,741	17,048	9 0
1911–12	39,167	18,158	9 3
1912–13	8,171	3,594	8 10
1913–14	28,886	13,933	9 8
1914–15	7,585	6,021	15 11
1915–16	11,582	13,062	22 7
1916–17	24,293	35,901	29 6
1917–18	38,108	88,453	46 5
1918–19	8,624	15,160	35 2
1919–20	29,425	40,045	27 3
1920–21	40,263	42,752	21 3
1921–22	16,922	14,792	17 6
1922–23	54,839	26,326	9 8
1923–24	98,684	65,290	13 3
1924–25	113,585	109,294	19 3
1925–26	105,643	89,334	16 11
1926–27	63,138	47,539	15 1
1927–28	122,419	65,451	10 8

It will be seen that during the season 1927–28, although a record total weight of fish was landed, the average price per 1 cwt. was, with the solitary exception of the season 1922–23, easily the lowest realised since the pre-war season of 1913–14. Thus, it is only necessary to refer back to the season 1925–26 to discover a total financial yield exceeding that of 1927–28.

It is of some local interest to note that the seasonal average price per 1 cwt. realised at Plymouth has almost always been greater than the yearly average price of herrings of British taking generally. This fact is brought out in the following table and in Fig. 1 :—

Year.	Herrings. British Taking. Average Price per 1 cwt. shillings.	pence.	Herrings. Plymouth only. Average Price per 1 cwt. shillings.	pence.	Season Dec.–Jan.
1906	8	1	4	11	1906–07
1907	5	1	5	6	1907–08
1908	5	7	11	10	1908–09
1909	6	0	6	1	1909–10
1910	7	8	9	0	1910–11
1911	5	11	9	3	1911–12
1912	6	2	8	10	1912–13
1913	6	4	9	8	1913–14
1914	6	9	15	11	1914–15
1915	16	5	22	7	1915–16
1916	21	11	29	6	1916–17
1917	22	10	46	5	1917–18
1918	24	6	35	2	1918–19
1919	14	1	27	3	1919–20
1920	11	11	21	3	1920–21
1921	4	7	17	6	1921–22
1922	7	1	9	8	1922–23
1923	7	11	13	3	1923–24
1924	11	4	19	3	1924–25
1925	10	5	16	11	1925–26
1926	8	7	15	1	1926–27
1927	9	5	10	8	1927–28

The daily returns of landings and market prices at Plymouth during December, 1927, provide a good illustration of the fact that the ruling price on the market is to a greater or lesser extent dependent upon the quantity of fish available. In the following table, daily landings have

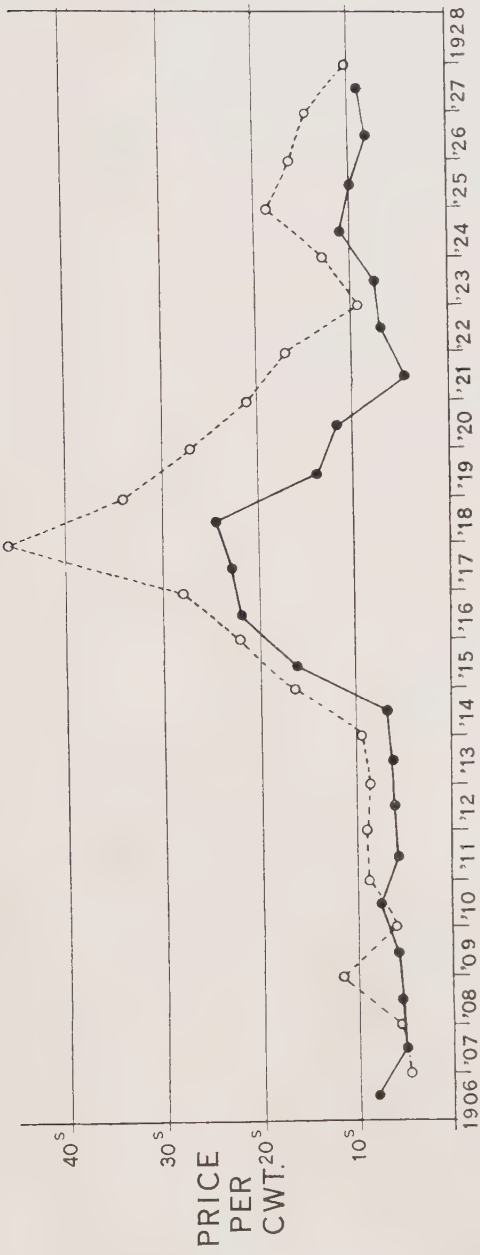

FIG. 1.—Market price per 1 cwt. of Herrings.
Continuous line —— Herrings of British taking throughout year.
Broken line ..... Herrings landed at Plymouth during Dec. and Jan.

been grouped into convenient classes and the average price per 1 cwt. calculated for each class :—

	Weight of Daily Landing (cwt.).									
	Less than 500	500 to 999	1000 to 1499	1500 to 1999	2000 to 2499	2500 to 2999	4000 to 4499	5000 to 5499	5500 to 5999	7000 to 7499
No. of Days	5	2	3	4	7	2	2	3	1	1
Total weight landed (cwt.)	1336	1409	3581	7140	15311	5750	8600	15818	5650	7010
Average weight (cwt.) per day	267	704·5	1194	1785	2187	2875	4300	5273	5650	7010
Average price per 1 cwt. (£)	1·186	·9645	·6782	·596	·566	·433	·483	·367	·256	·320

In Fig. 2 the average price per 1 cwt. for the average weight in each class has been plotted, and the smooth curve AB drawn freehand to provide a reasonably good representation of the general downward trend of the average price as the size of the daily landing increases. It is seen that this curve falls steeply at first, but less and less rapidly later. By erecting perpendiculars from the correct points along the base line, to cut the curve AB, it is possible to read off the average price per 1 cwt. for landings of given size. The following data have been obtained in this manner :—

Weight of landing (cwt.)	500	1000	2000	3000	4000	5000	6000	7000
Approx. average price per 1 cwt. (shillings and pence)	20/–	15/–	11/6	9/11	8/6	7/4	6/3	5/4
Approx. average price per 1 lb. (pence)	2·1	1·6	1·2	1·1	·9	·8	·7	·6

It is also of interest to note that during December, 1927, on 15 out of the total of 30 days on which fish were actually landed, a total of 48,085 cwt., representing about 67% of the total weight landed throughout the month, was sold at a daily average price varying from 10s. to 5s. per 1 cwt. ; that is, at the rate of from 1d. to ½d. per 1 lb.

In applying these statistics, however, it must be borne in mind that they are *averages ;* they smooth over those differences in price, often appreciable, between different sales on the same day. Every prospective buyer knows his own immediate requirements, and bids accordingly. One needs a given quantity of fish of the finest quality procurable for which he is prepared to pay a high price. Having secured these fish, he is indifferent to all subsequent sales. On the other hand, a second buyer is not likely to compete for fish until the price has fallen to a certain figure, but he will then buy heavily. The average figures for the day used in the foregoing considerations thus represent the mean of individual sale prices which may differ to a marked degree, so that in drawing comparisons such as that between prices at the source and those paid by the consumer these averages must be applied with great caution, if at all.

So far as actual fishing and marketing operations are concerned, however, they are instructive. By utilising the data derived from the curve AB on Fig. 2 we can determine the approximate total market value of a day's catch of given weight; thus :—

Weight of landing (cwt.)	500	1000	2000	3000	4000	5000	6000	7000
Approx. average price per 1 cwt. (shillings and pence)	20/–	15/–	11/6	9/11	8/6	7/4	6/3	5/4
Approx. total value of landing (£)	500	750	1150	1485	1700	1835	1875	1875

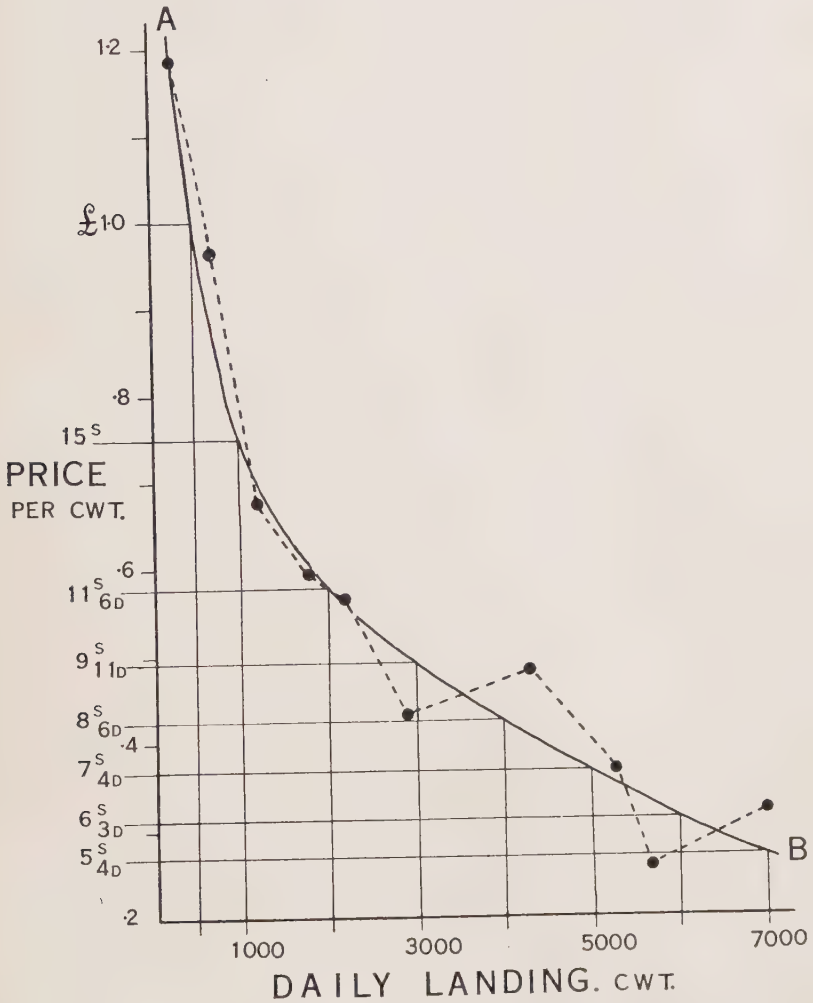

Fig. 2.—Market price per 1 cwt. of Herrings landed by steamers during Dec., 1927.

The continuous curve AB is drawn freehand as an approximate fit to the observed values, and from it the price per 1 cwt. for a daily landing of given size may be estimated.

To the mind of the fisherman these figures mean that during December, 1927, in increasing the total weight of fish landed in a day from 1000 cwt. to 2000 cwt., he received £400 for the additional 1000 cwt., whereas in raising the daily total from 4000 cwt. to 5000 cwt., the remuneration he received for the additional 1000 cwt. had dwindled to £135. And what is more, any amount of fish in excess of 5000 cwt. per day was literally given away.

These figures also suggest that during this period buyers were not prepared to spend much more than £1800–£1900 on daily catches aggregating 5000 cwt. or over.

The Characters of the Fishes Landed.

Eleven samples from commercial landings between October 17th, 1927, and March 3rd, 1928, were examined for length, sexual condition, age, and growth. The possession of corresponding data for the three preceding seasons undoubtedly adds to the interest and value of the present records, enabling useful comparisons to be made from which a more intelligent view of events from year to year can be obtained.

Average Length.

In Table I on page 23 the values of the median length (Q_2), the quartiles (Q_1 and Q_3), and the upper and lower limits of size for each sample are given. Corresponding data for previous seasons were given in Part III (Ford, **2**, p. 301). The means of the individual values of Q_1, Q_2, and Q_3 for each season provide a rough indication of the length distribution, and in the following table these means for the period November to January during the four consecutive seasons are shown :—

	Mean of sample values for the following seasons (Nov.–Jan.).			
	1924–25.	1925–26.	1926–27.	1927–28.
		(cm.).		
Q_1 . . .	26·4	26·4	25·6	24·7
Q_2 . . .	27·3	27·4	26·5	25·8
Q_3 . . .	28·2	28·3	27·8	27·0

It is seen that the appreciable depression of length during 1926–27 was followed by a further drop during 1927–28. It is true that considerable differences in average size can be occasioned by changes in the size of mesh in the drift-nets used (*vide* Hodgson, **3**), but in the present instance this is not thought to be the important factor. The account of the age-composition of the samples, given later, will demonstrate convincingly that the 1927–28 samples included a very much larger percentage of young fishes than those of 1925–26 or even 1924–25. Further discussion of the length data will be found on page 12 in conjunction with those on age.

Age Composition of Samples.

The age composition of the 1927–28 samples is given in the form of percentages in Table II on page 24. These results are also shown graphically in Fig. 4 on page 11, while, for convenience, the corresponding results for previous seasons have been republished in Fig. 3. It will be noticed that the principle used during the seasons 1924–25 and 1925–26, namely, of including all fishes definitely older than " 6 zones 6 rings " in a composite year-group, has been reverted to. Where interest is chiefly centred on the percentages of well-represented year-classes which either form the mainstay of a current fishery or will become increasingly important in the near future, it is hardly necessary to estimate precisely the age of a few older fishes.

By determining the mean of the individual sample percentages of each year-group, we can arrive at an average composition which will serve as a working summary for the season. Admittedly, such a summary is an approximation, but it facilitates the comparison of results from season to season ; it is not intended to stand as an accurate assessment of the age-stock on the grounds. The summary for 1927–28 is as follows :—

Season (Nov.–	Percentage Composition by Age.										Older than
Jan.).	2	2–3	3	3–4	4	4–5	5	5–6	6	6–old	6
1927–8	—	—	16·5	0·2	19·2	1·2	30·4	1·8	11·1	1·1	18·2

As an alternative, sample age-data may also be summarised as percentages of definite year-classes, thus :—

Season	Percentages of Year-classes.				
(Nov.–Jan.).	1925	1924	1923	1922	1921 & earlier.
1927–28 . .	16·5	19·2	30·4	11·1	18·2

It is seen that the 1923 year-class, now as 5-zoned 5-ringed fishes, definitely dominated with a percentage of 30·4. This is in accordance with the expectation expressed in Part III (Ford **2**, p. 291) when the previous season's results were under review. Two other facts should be noted at this stage. In the first place, there was an unusually high percentage of 3-zoned 3-ringed fishes (1925 year-class), the significance of which will be dealt with later. Secondly, the year-class 1920, so dominant a constituent of the samples from the landings of the three previous seasons, no longer formed an important element.

The Year-class 1920.

It has previously been shown that fishes of the year-class 1920 were much in evidence during the seasons 1924–25, 1925–26, and 1926–27 (Ford, **2**, p. 289). As 5-zoned 5-ringed fishes in 1924–25 they comprised

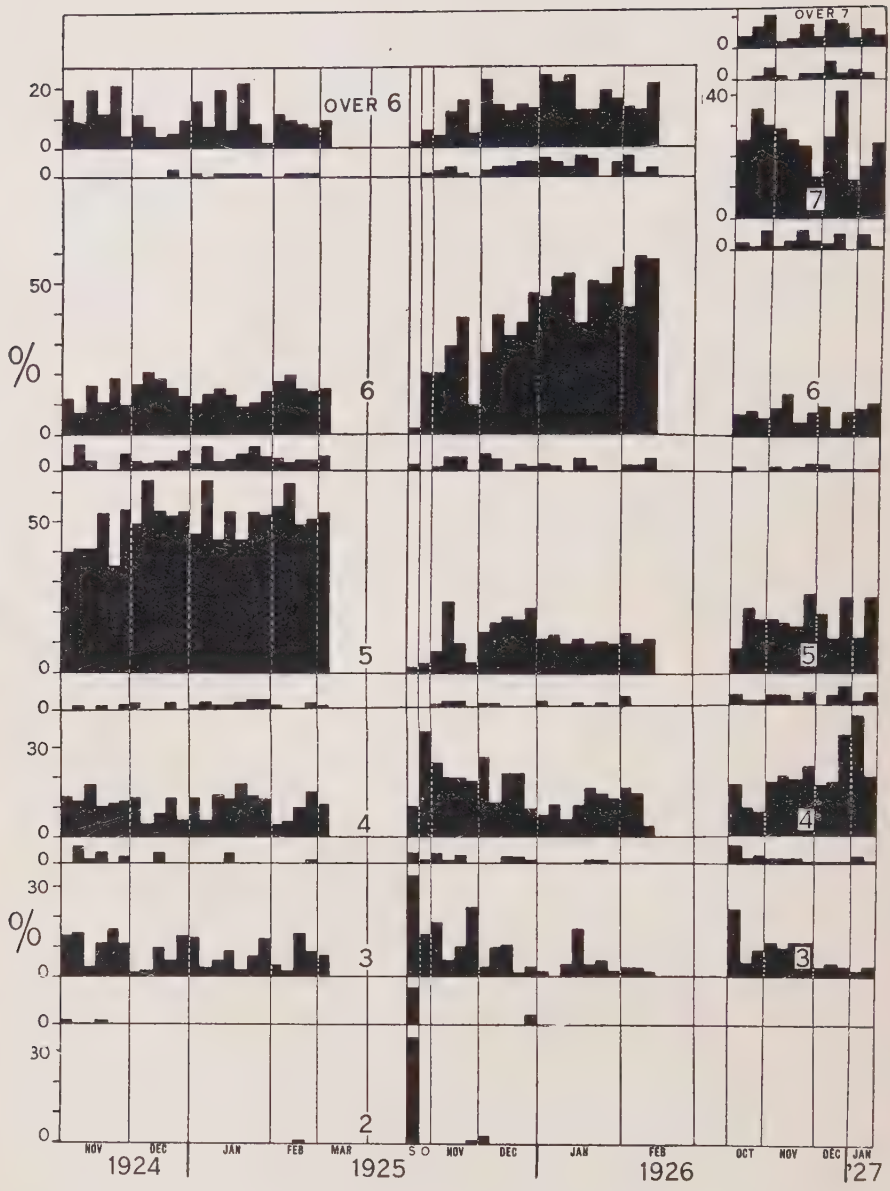

FIG. 3.—Age composition of samples of Plymouth Herrings.

Sample percentages are shown as small vertical blocks. The age-classes are as follows:

2	2-zoned 2-ringed.
3	3-zoned 3-ringed.
4	4-zoned 4-ringed.
5	5-zoned 5-ringed.
6	6-zoned 6-ringed.
7	7-zoned 7-ringed.

The "interval" classes are obviously 2 or 3, 3 or 4, 4 or 5, etc.

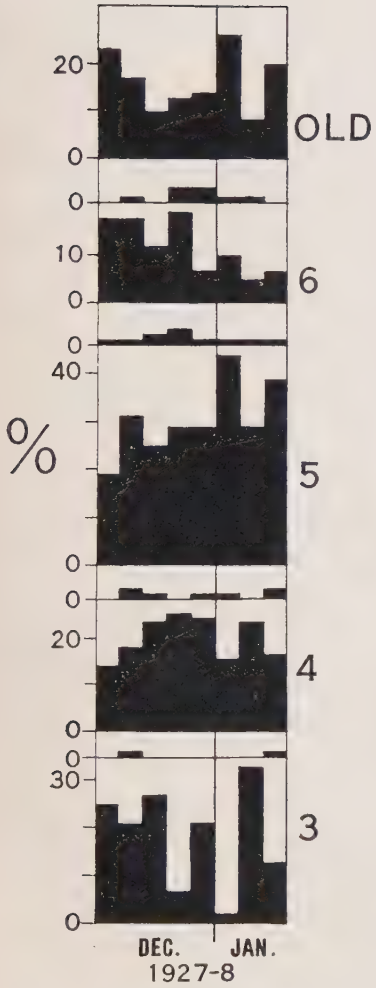

FIG. 4.—Age composition of samples of Plymouth Herrings landed during season 1927–28.

Figure constructed in same way as Fig. 3. The age-class "OLD" includes all fishes definitely older than 6-zoned 6-rings.

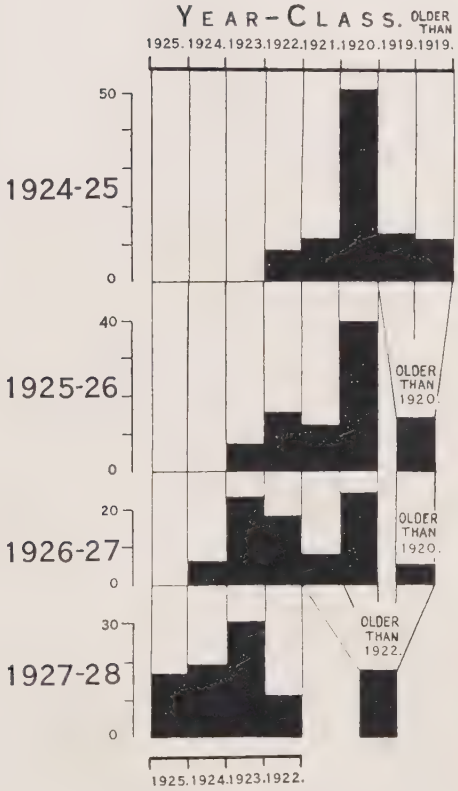

FIG. 5.—Summary of age composition during four consecutive seasons at Plymouth. The average seasonal percentage of each year-class is shown as a small vertical block.

more than 50% of many samples ; as 6-zoned 6-ringed fishes in 1925–26 they again greatly outnumbered those of any other year-class, while as 7-zoned 7-ringed individuals in 1926–27 they were still a leading element although not so heavily represented as in previous years. But now, in 1927–28, as 8-zoned 8-ringed fishes they no longer form a dominant constituent of the samples, having been replaced by the members of younger year-classes. It is, naturally, a little disappointing that the available data do not go sufficiently far back actually to cover the whole period throughout which this successful year-class 1920 had formed part of the Plymouth catches. Judging from recent experience, it seems extremely unlikely that more than an occasional well-grown individual of this class would have been caught in 1921–22 as a 2-zoned 2-ringed fish. It is possible, however, that in the following season of 1922–23, the catches would have included an appreciable percentage of the 1920 year-class as 3-zoned 3-ringed fishes. Furthermore, when as a result of a further year's growth their size has become well within catchable range, the percentage in 1923–24 as 4-zoned 4-ringed individuals might easily have exceeded that of any other year-class represented.

Length for Age.

In the following table the average length and individual variation for fishes of the year-classes represented during the season 1927–28 are given :—

Year-class.	Age.	No. of fishes in each of 10 length-groups (cm.). 21	22	23	24	25	26	27	28	29	30	Total No.	Average length. cm.
1925	3-zoned 3-ringed	4	18	57	71	34	4	1	1	–	–	190	24·2
1924	4-zoned 4-ringed	–	2	26	49	66	32	9	3	1	1	189	25·3
1923	5-zoned 5-ringed	–	–	2	25	120	105	44	5	–	–	301	26·1
1922	6-zoned 6-ringed	–	–	–	7	27	31	31	8	5	–	109	26·7

These averages are lower than the corresponding ones for previous seasons (cf. Ford, **2**, p. 293), particularly those of the 3-zoned 3-ringed and 6-zoned 6-ringed fishes. The fact that fishing during 1927–28 was conducted almost entirely on the more easterly grounds may account for this (*vide* Ford, **2**, p. 287).

Predictions of Future Fisheries.

No one with any practical experience of the annual fluctuations to which the herring fisheries are subject, will be likely to underestimate the difficulties which have to be overcome before there can be any hope of giving reliable forecasts of future fisheries. In the pages which follow an attempt has been made to indicate how the results of the investigations during the past few seasons may be brought to bear directly upon this

practical question. In the face of so formidable a problem, any worker might reasonably hesitate to advance suggestions after such a short period of study ; it should, therefore, in fairness to the present writer, be clearly recognised that the attempted forecasts are given primarily as illustrations of the way in which the limited data may prove helpful, and, secondarily, as trial predictions which can ultimately be substantiated or disproved. Even if such forecasts do eventually prove poor, they should not necessarily be regarded as a condemnation of the whole work ; the discrepancies between forecast and reality ought rather to be examined most carefully in an endeavour to discover why they have arisen.

If we examine the data of landings by steamers over a period of years at Plymouth we are at once impressed by three facts :—

1. The average weight per landing varies greatly from one season to the next.
2. In some years the heaviest landings are made in December, whereas in others, in January.
3. Fishing operations are adversely influenced by bad weather conditions.

Of these three facts, the present work can only deal with the first two : the influence of meteorological conditions is outside its scope, important as it may be. We have thus to discuss how the systematic study of the fishes landed during the past four seasons, and of a set of temperature records in the Plymouth area over the same period, can help us to predict the yield of a future fishery, as well as the " earliness " or " lateness " of the fishery in that season.

We have already seen that the 1920 year-class of fish formed a marked percentage of the landings in recent years. Let us, therefore, first notice the state of the fishery during those seasons when this year-class was represented in the landings. In the following table, the values of the average weight per landing by steamers are shown against the corresponding age and percentage of fishes of the 1920 year-class :—

Season (Nov.–Jan.).	1920 Year-class. Age. Zones.	Rings.	Percentage.	Average Weight per Landing by Steamers. cwt.
1921–22	2	2	Practically unrepresented	13·8
1922–23	3	3	No data available	25·8
1923–24	4	4	No data available	37·8
1924–25	5	5	50·5	40·0
1925–26	6	6	39·6	23·0
1926–27	7	7	24·2	16·0
1927–28	8	8	< 10	46·6

We see that the average weight per landing rose each season from 1921–22 to 1924–25, but then fell away for two seasons in succession. During the same period the percentage of the 1920 year-class rose and fell in a corresponding manner. It is not unreasonable to argue that this is no mere coincidence and that the high average landings during 1923–24 and 1924–25 were the result of the maximum representation of a highly successful year-class 1920. From this observation we could reasonably contend that had we in 1922–23 appreciated the coming importance of this year-class we could have predicted the good catches in 1924–25 and 1925–26.

Clearly, then, as an initial step towards forecasting, we must examine our data on age composition, in order to get as much information as possible concerning the various year-classes represented.

Age Composition of Samples during the four Seasons from 1924–25 *to* 1927–28.

In the following table, and in Fig. 5 on page 11, the average age composition for each of the four seasons 1924–25 to 1927–28 is given. The seasonal averages are in each case the mean of all the sample percentages of that season, and they are tabulated according to the year-class :—

Season (Nov.–Jan.)	Average Percentage of different Year-classes.							
	1925	1924	1923	1922	1921	1920	1919	Earlier than 1919
1924–25	—	—	—	8·2	11·8	50·5	12·8	11·0
1925–26	—	0·25	7·2	15·7	12·6	39·6	14·2	
1926–27	—	6·3	23·2	18·9	8·6	24·2	5·2	
1927–28	16·5	19·2	30·4	11·1			18·2	

3-zoned 3-ringed
4-zoned 4-ringed
5-zoned 5-ringed
6-zoned 6-ringed

Before proceeding to examine the actual data given in the above table, it will be helpful to point out the three leading ways in which the data may be read :—

1. By reading along a horizontal line we obtain the percentage of each year-class during the same season.
2. By reading down a vertical column we learn how the percentage of a given year-class changes from one season to the next.
3. By reading across the diagonal rows we learn the percentage of fishes in each season having a given number of zones and rings.

Turning now to the data themselves, we see, in the first place, that a year-class usually makes its initial appearance in the samples when 3-zoned 3-ringed. The 1924 year-class was an exception, but even then only an occasional 2-zoned 2-ringed fish occurred in 1925–26. Bearing in mind the relatively small size of fishes when 3-zoned 3-ringed, it is probable that as yet only the bigger representatives are caught, the smaller ones avoiding capture by passing through the mesh of the net.

In the second place, the percentage of a year-class tends to rise until its members have become 5-zoned 5-ringed. For example, in 1925–26, the percentage of year-class 1923, then 3-zoned 3-ringed, was 7·2%; in the following season, when the fishes were 4-zoned 4-ringed, the percentage rose to 23·2%; in 1927–28, when the fishes had become 5-zoned 5-ringed, the percentage had again risen to 30·4%. Year-classes 1921, 1922, and 1924 show a similar tendency (see Fig. 5 on p. 11).

Thirdly, the percentage of a year-class tends to decline when its members have passed the age of 5-zones 5-rings. Thus, in 1924–25, the percentage of year-class 1920 was 50·5%, the fishes being 5-zoned 5-ringed; in 1925–26 the percentage of the same year-class, now 6-zoned 6-ringed, had dropped to 39·6%; in 1926–27, when the fishes were 7-zoned 7-ringed, the percentage had dropped still farther to the low level of 24·2%; in 1927–28 the percentage of year-class 1920 had become so reduced that by including with it the percentages of all older year-classes, as well as that of year-class 1921, the aggregate was only 18·2%. The percentages of year-classes 1919, 1921, and 1922 also showed a decline after the age of 5-zones 5-rings was reached (see Fig. 5, p. 11).

Let us now return to the 1927–28 data. Five distinct age-groups are concerned, viz.: the four year-classes 1925, 1924, 1923, and 1922, and the composite group which includes all fishes of the years prior to 1922. Arguing on the indications arrived at above, we can make some progress if asked to predict what will happen during the next few seasons. We will consider each age-group in turn:—

(A) Year-class 1925.

Members of this class, as 3-zoned 3-ringed individuals, formed 16·5% during the season 1927–28. It will be observed that this percentage was

considerably greater than that for similar-aged fish in any of the preceding seasons, indicating that the year-class 1925 is likely to prove a highly successful one. We should expect that during the season 1928–29, when the fish will be 4-zoned 4-ringed, the percentage will prove appreciably higher—perhaps from two to three times that shown in 1927–28. In the following season of 1929–30, when the members of this same year-class will be 5-zoned 5-ringed, we may look for a percentage greater even than that of 1928–29—perhaps amounting to 50% of the total sample. In the next season (1930–31), when an age of 6-zones 6-rings will be reached, we may expect to witness the beginning of a decline in importance, which decline will in subsequent seasons become more and more pronounced.

(B) Year-class 1924.

Members of this class, as 4-zoned 4-ringed individuals, formed 19·2% during the season 1927–28, a value which compared fairly favourably with that for fishes of corresponding age in previous seasons. We should expect in 1928–29 a somewhat increased percentage, say approaching 25%. In the following season (1929–30) the first evidence of a falling-off in numbers would be anticipated, for the fishes will then have become 6-zoned 6-ringed. In the next season (1930–31) the percentage will probably have become reduced to an amount hardly large enough to be considered an important element of the catches.

(C) Year-class 1923.

Fishes of this class, as 5-zoned 5-ringed individuals, comprised 30·4% during the season 1927–28. This percentage must be regarded as the highest likely to be reached by this year-class. The first signs of depletion are to be looked for in 1928–29, although the percentage then reached should still form an appreciable constituent of the samples. In 1929 30, a further reduction would be expected, while in 1930–31 this year-class will probably cease to be more than nominally represented.

(D) Year-class 1922.

This year-class had already passed its zenith in 1927–28, so that in 1928–29 it cannot be expected to enter much into the landings.

(E) Year-classes of 1921 and earlier years.

As with year-class 1922, these year-classes had in 1927–28 already passed out of the stage when they could be considered likely to continue as important constituents of the landings.

If we take as a criterion of relative importance a percentage of 10%, we can, from the observations made under (A) to (E), suggest the future

season during which each of the year-classes represented in 1927–28 will cease to be an important element of the samples :—

Year-classes of 1921 and earlier years	During season	1928–29
Year-class 1922	,,	,,	1928–29
Year-class 1923	,,	,,	1929–30 or 1930–31
Year-class 1924	,,	,,	1930–31
Year-class 1925	,,	,,	1931–32 or 1932–33

Thus by 1932–33, i.e. five seasons hence, practically the whole of the stock represented in this season of 1927–28 will have been replaced by new stock.

It is important to realise, however, that no consideration of the sample data for any given season can yield the slightest information concerning the proportion of new year-classes which will appear in the future. But, by watching the actual percentage of 3-zoned 3-ringed fishes in each season, we can obtain advanced warning of the part likely to be played by a newly arrived year-class. If the percentage of 3-zoned 3-ringed fishes is unusually high, we may expect fishes of that year-class to become a leading constituent of the landings during the next two seasons at least ; if, on the other hand, 3-zoned 3-ringed fishes are relatively few, we shall not expect great subsequent yield from that year-class.

Age Composition in Relation to Density of Landings.

In the preceding section we endeavoured to predict the proportions of the different year-classes in samples of future seasons. We have next to discuss the probable effects of these changes in proportion on the density of commercial landings. At this stage it is necessary for us to recall that in our age-estimates we are dealing with percentages and not absolute values. Thus to determine the numerical abundance of fishes of a given year-class in a particular season, we must interpret our age-percentages in terms of the absolute density of fish—in our case, the average weight per landing by the steamers. With these two sets of data available, let us try first to sum up the situation during the season 1927–28, when the average weight per landing rose to a new high level. (See table on p. 13.) We can safely conclude that the good landings in that season were not due to the year-classes 1920 and 1921, for the former had at that time become seriously depleted, while the latter had been poorly represented during the two previous seasons when most would be expected from it. Evidence seems in favour of the view also, that year-class 1922 was of minor importance ; had it been one of appreciable success we should not have expected the average weight per landing in 1926–27, when fishes of this class were 5-zoned 5-ringed, to have fallen so low as 16 cwt. Our

attention is thus attracted particularly to year-classes 1923, 1924, and 1925. Of these three, year-class 1923 had already given promise in 1926–27 of being a more important one than its immediate predecessors of 1921 and 1922, and the possibility of an increase in its significance in 1927–28 was suggested in an earlier Report. (Ford, **2**, p. 291.) Here again, however, the low average landing in 1926–27 does not support the view that year-class 1923 was an outstanding success like that of 1920, although it must be regarded as a considerable improvement on year-classes 1922 and 1921 on account of its importance during 1927–28.

Turning next to year-class 1924, we note that its members, as 4-zoned 4-ringed fishes during the season 1927–28, contributed 19·2% towards the high average landing of 46·6 cwt. We must therefore regard this year-class as of at least average importance, and expect it to yield a satisfactory quota to catches of the immediate future. The percentage of 6·3 in 1926 27 when the fishes of the class were 3-zoned 3-ringed, however, did not arouse unusually high expectations.

The third of the classes to be considered is that of 1925 which appeared for the first time in appreciable numbers in 1927–28. Here we have very real hopes of a new highly successful group which in the first year of appearance constitutes a percentage of 16·5% of a high seasonal yield.

We are now in a position to attempt a forecast for the forthcoming season of 1928–29. On the indications considered above, we should expect the following :—

1. A decline in the abundance of the fairly rich year-class 1923.
2. An increase in the fairly rich year-class 1924.
3. An increase in the rich year-class 1925.

We should, under the circumstances noted, expect that the total increase resulting from (2) and (3) would more than counterbalance the decrease due to (1). That is to say, so far as the old stock is concerned, there should be a better available supply of fish in 1928–29 than in 1927–28. Furthermore, an additional new element, the 1926 year-class, should appear as 3-zoned 3-ringed fishes, but no forecast can, at present, be offered concerning the extent to which this may be expected. Altogether, then, so far as the available supply of fish is concerned, the prospects for the season 1928–29 would appear favourable.

Early and Late Seasons.

It is well known that at Plymouth, as elsewhere, the season is sometimes early, sometimes late. Any form of observation which would give a reliable indication of the time at which good fishing might be expected in an impending season, would, therefore, be of material practical utility.

We know that, at Plymouth, the shoals which arrive in the winter are concentrating for spawning. It is reasonable to think that such a physical factor as the temperature of the sea will influence the development and ultimate maturation of the roes and milts, and, in consequence, will have its effect on the time at which the fishes approach the spawning-grounds. Since the year 1921, regular observations of temperature at certain hydrographical stations in the Plymouth area have been made by Dr. Atkins and Mr. Harvey of the Laboratory Staff. We may safely use the data on temperature at a depth of 10 metres at Station E_1

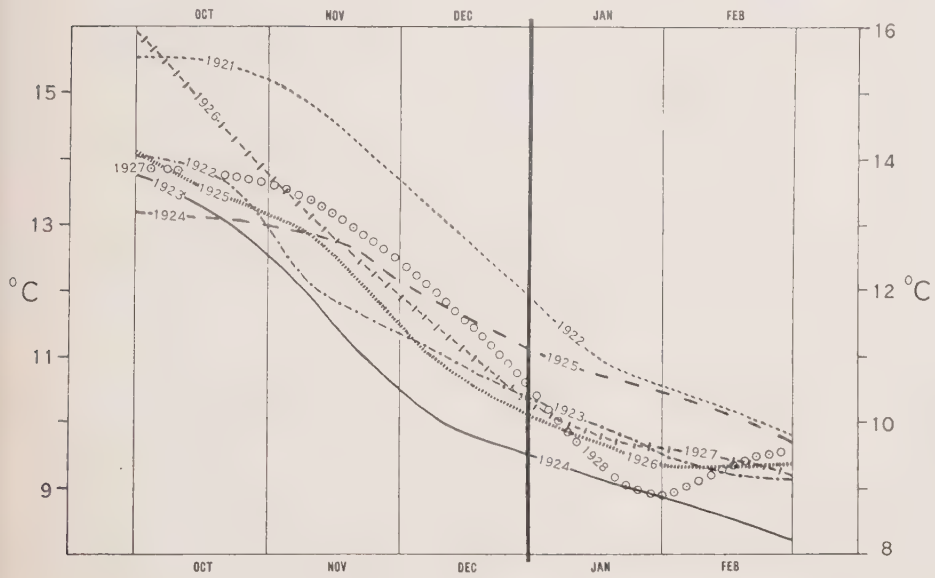

Fig. 6.—Temperatures at 10 metres depth at Hydrographical Station E_1.

(ca. 10 miles S.W. of the Eddystone) as an approximation to the temperature conditions prevailing over the Plymouth herring fishing-grounds (*vide* Ford, **2**, p. 287). In Fig. 6 the temperatures during the winter months are expressed in the form of smoothed curves drawn to fit the data.

From the curves in Fig. 6, the following average values for the seven seasons have been determined :—

Date.	Nov. 1st.	Dec. 1st,	Jan. 1st.	Feb. 1st.
Average temp. (°C)	13·5	11·9	10·5	9·6

Comparing the records for individual seasons with the above averages, we see at once that during 1921–22 the temperatures were much above the normal throughout the months of November, December, and January,

whereas during 1923–24 they were consistently below the normal. It is of immediate interest to examine the monthly landings of herrings during these two markedly abnormal years. For this purpose, the landings by motor-drifters are the more convenient, for these vessels are at work during November, whereas the steamers rarely arrive in numbers until December. Here are the data of landings by motor-drifters during the two seasons 1921–22 and 1923–24 :—

Season.	Total Weight of Fish Landed by Motor-Drifters. (Cwt.) November.	December.	January.
1921–22	293	2,103	4,325
1923–24	23,492	23,840	17,325

The contrast between these two sets of data is striking. In the first place it is seen that the total landed during November was almost negligible in 1921–22 but of real importance in 1923–24. This observation becomes of additional interest when it is realised that in the month of November, during each of the remaining five of the series of seven seasons, the total weight landed never once exceeded 9000 cwt., nor was it less than 4000 cwt. In the second place it is seen that in 1921–22 the greatest quantity of fish was landed as late as January, whereas in 1923–24 the best catches were taken in November and December.

There appears to be no evidence that these two facts can be entirely explained by differences in intensity of fishing due to the number of vessels working in the two seasons, or to varying weather conditions. Turning to the temperature records, therefore, it is interesting to notice that the temperature range during January, 1922, corresponded with that prevailing during the greater part of November, 1923. From this we may well suppose that catches are likely to be considerably better in waters *below* 12° C. than in waters *above* 12° C. in temperature.

Referring once more to Fig. 6, we see that the temperatures prevailing during the season 1924–25 are interesting in that the curve, like those for 1921–22 and 1923–24, is a departure from the normal, although of a different character. The water during late December and the whole of January was appreciably warmer than usual. Thus on January 1st, 1924, the temperature was about 11·1° C. compared with the normal of 10·5° C., and on February 1st it was still as high as 10·5° C., compared with the normal of 9·6° C. Comparing the average weight of fish per landing by the steamers during December, 1924, and January, 1925, we find that the average was higher during the latter month (Dec., 1924=20·3 cwt., Jan., 1925=50·7 cwt).. That is to say, superior catches coincided with a temperature lower than about 11·1° C.

From these observations concerning three seasons abnormal so far as temperature is concerned we may, therefore, draw up an experimental

progress report regarding the yield of the fishery with respect to the temperature of the sea :—

Temperature °C.	Expected Yield.
Above 13	poor.
13–12	improving.
12–11	fair.
Below 11	good.

Assuming that this report is sound, we can, from the temperatures representing the average conditions for the seven seasons (given on p. 19),

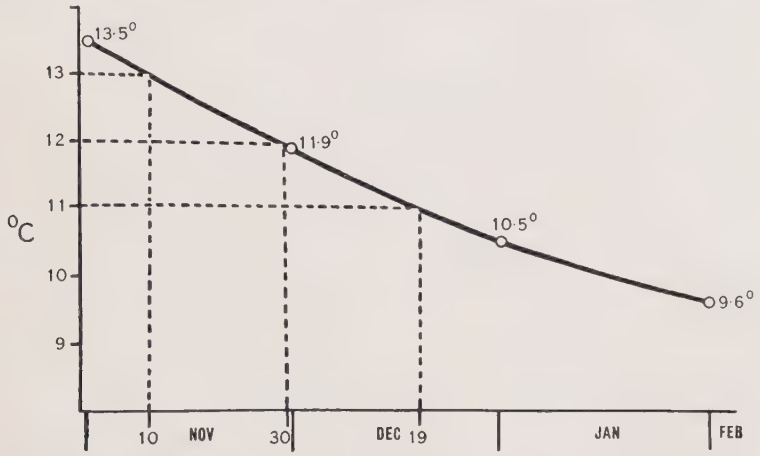

Fig. 7.—Average temperatures at 10 metres depth at Hydrographical Station E_1, based on the seven seasons' data given in Fig. 6. The dates at which 13° C., 12° C. and 11° C. are reached are indicated.

deduce a hypothetical "normal" time table of fishing. In Fig. 7, a smooth curve has been drawn to pass through the calculated average temperatures, from which we can determine the dates at which the criterion temperatures are reached :—

13° C.	12° C.	11° C.
November 10th.	November 30th.	December 19th.

We should therefore expect fishing normally to be poor until November 10th ; improving from November 11th to November 30th ; fair from December 1st to December 19th, and to become really satisfactory on December 20th.

Future Investigations.

In the above sections an attempt has been made to demonstrate the application of the study of the age of herrings, and the temperature conditions on the fishing-grounds to the question of the prediction of

future fisheries. It has been shown that advanced knowledge of the probable abundance of fish in a future season can be obtained by the study of the age of fishes in earlier years in conjunction with statistical data on market landings. Clearly, then, similar work should be carried out in the seasons which are to come in order to verify or improve upon the conclusions so far reached. With regard to the prediction of a "time table" of fishing, there is good reason to advocate the observation of temperature over the fishing-grounds at short intervals, from, say, the beginning of November onwards, so that more precise data may be obtained concerning the coincidence of fishing results with water temperature.

It is hardly necessary to point out that there are factors likely seriously to influence local fishing which in these pages have not been taken into account at all, such as variations in strength and direction of winds; the changing tides, or the phases of the moon. While we know with certainty that gales frequently prevent the smaller vessels from leaving harbour, and that wind and tide materially affect actual fishing operations, we do not, as yet, possess much knowledge concerning the effect of such factors on the fish themselves. Conceivably, it is possible that fish may be present in the vicinity in good quantity, although few can be caught. For instance, do fish react to a period of calm sea over the time of "dead" tides?—Do they, as one experienced skipper suggests, keep to the bottom owing to the resulting clearness of the water? If a wind now arises, will it "stir the fish" and so cause better fishing? Is an offshore (north-easterly) wind bad for fishing? Does the light of a full moon induce the fish to take to the deeper layers? Such questions as these remain to be solved, but the solutions will be hard to accomplish on account of the practical difficulties in observation.

There is also the question of the particular local grounds on which fish are plentiful in one year, or during one part of the season, and not in another. Why, for example, are fish located comparatively far up Channel towards Brixham, in one season, and away down Channel to the westward of Plymouth in another? Can these variations be accounted for and thus predicted? It is suggested that the study of growth from scale-measurements, and the comparisons between fishes from different parts of the Channel and south-western district will lead to a fuller knowledge of the origin and movements of the herring shoals visiting Plymouth, and that this information should ultimately indicate the particular local grounds likely to be frequented by shoals of known character. This accomplished, the further work of anticipating the future stock for these particular grounds can be undertaken. In this connection the study of fishes landed at Brighton, Brixham, Mevagissey, Newlyn, Padstow, and Milford, during the past few years has provided data of immediate value.

Finally, there remains the study of the circumstances which control the survival of the yearly broods of young herrings resulting from the spawning of the visiting shoals, for until we are fully acquainted with these facts, we cannot foretell what amount of new stock will arrive in a future season. This necessitates the detailed investigation of the history of the fish from the egg until the age of three years is reached, and, also, of the physical and other conditions which determine the number of fishes which will survive to enter the adult shoals. It is only in this way that we can arrive at an explanation of the amazing success of some year-classes and the complete failure of others; while, as has already been shown, knowledge in advance of outstanding year-classes is also knowledge in advance of fishing prospects.

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TABLE I.

Length Distribution (cm.).

Sample.	Date. 1927	Total No. of Fishes	Lower Limit.	Lower Quartile Q_1	Median Q_2	Upper Quartile Q_3	Upper Limit.
1	Oct. 17	100	23·5	24·6	25·4	26·2	28·5
2	Nov. 10	110	24·5	26·0	26·6	27·5	30·5
3	Dec. 2	110	21·5	25·0	26·0	27·1	30·5
4	Dec. 8	110	23·5	24·9	25·9	27·4	29·5
5	Dec. 14	100	22·5	24·4	25·6	26·6	29·5
6	Dec. 21	100	22·5	24·1	25·2	26·5	29·5
7	Dec. 30	100	22·5	24·4	25·3	26·6	30·5
	1928						
8	Jan. 2	110	24·5	25·9	26·7	27·6	29·5
9	Jan. 17	100	21·5	23·5	24·7	26·1	30·5
10	Jan. 28	100	22·5	24·1	26·0	27·4	29·5
11	Mar. 3	100	22·5	25·2	26·4	28·1	31·5

TABLE II.

Percentage Age Composition.

Sample.	Date. 1927	2	3	3–4	4	4–5	5	5–6	6	6-old.	Older than 6	?	Total No. of Fish in Sample.
1	Oct. 17	4	41	–	14	–	23	1	8	–	9	–	100
2	Nov. 10	–	–	–	15	4	29	5	14	–	32	1	100
3	Dec. 2	–	25	–	14	–	19	1	18	–	23	–	100
4	Dec. 8	–	21	1	18	2	31	1	8	1	17	–	100
5	Dec. 14	–	27	–	23	1	25	2	12	–	10	–	100
6	Dec. 21	–	7	–	25	–	29	3	19	3	13	1	100
7	Dec. 30 1928	–	21	–	24	1	29	1	7	3	14	–	100
8	Jan. 2	–	1·8	–	15·5	0·9	43·6	0·9	10·0	0·9	26·3	–	110
9	Jan. 17	–	33	–	23	–	29	1	5	1	8	–	100
10	Jan. 28	–	13	1	16	2	39	1	7	–	20	1	100
11	Mar. 3	–	11	–	12	–	36	1	8	4	27	1	100

Herring Investigations at Plymouth. VI. Winter Herrings Caught off the Sussex Coast and in the Great West Bay during the Years 1924 to 1927.

By

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With 2 Figures in the Text.

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INTRODUCTION.

As explained in Part I of this series of Reports (Ford, **1**, p. 238) it was thought that the study of herrings landed at other ports would provide information bearing upon the question of the origin and migrations of the shoals visiting Plymouth during the winter. The examination of the appreciable number of such samples obtained, however, has yielded results which are of interest in themselves, apart from their application

to the question of the Plymouth fishery. In this paper, an account is given of the study of herrings landed at Hastings and Brighton from off the Sussex coast, and at Brixham from the Great West Bay. It is necessary to point out that the sampling was not specifically designed for such a study, so that due allowance for this fact must be made in drawing conclusions as to the progress of the local fisheries.

I am indebted to the following gentlemen for their kindness in forwarding samples to Plymouth :—

	Samples from
Mr. Edward Page, Chief Fishery Officer, Sussex.	Hastings.
Mr. H. W. Jordan of Brighton	Brighton.
Mr. T. B. Lovell of Brixham	Brixham.

Herrings Caught off the Sussex Coast.

During the months of October, November, and December, herrings caught in drift or standing nets in local waters by small craft are landed at ports or on beaches along the Sussex coast. A total of 9 samples taken in this area during the seasons 1924 to 1927 was examined, and data collected regarding length, age, growth, sexual condition, and average number of vertebræ.

Condition of Gonads (Roes and Milts).

The examination of the gonads showed that the samples consisted overwhelmingly of " full " fishes, with occasional ripe, spent or immature individuals. Actual spawning, therefore, would hardly be expected to occur until at least the end of December. The youngest fishes (3-zoned 3-ringed) possessed well-advanced gonads, so that it is reasonable to suppose that first spawning may commonly occur during the third winter of life in the scaled condition.

Average Length.

The values of the median (Q_2) and quartiles (Q_1 and Q_3) for each sample are given in Table I on page 39. The range in length of the middle 50% (Q_3–Q_1) may again be used as a convenient index of the commonest sizes (cf. Ford, III, p. 287). It is seen that Q_1 varied from 22·1 cm. to 23·2 cm., and Q_3 from 23·8 cm. to 24·7 cm. ; that is to say, fishes of the 22, 23, and 24 cm. groups always comprised at least 50% of each sample. It was shown in Part III (Ford, **1**, p. 287) that the Plymouth winter fishery is centred chiefly upon herrings of the 25, 26, 27, and 28 cm. groups, so that here on the Sussex coast the fishery is based upon much smaller fishes.

Age Composition of Samples.

The estimates of age from scale readings are given in Table II on page 40 in the form of percentages and in graphic form in Fig. 1. It is clear that, throughout, the bulk of a sample was made up of 3-zoned 3-ringed or 4-zoned 4-ringed fishes. This suggests that, in each season, the landings include a considerable proportion of new stock, and, also, that much of the old stock remaining from a previous season either does not subsequently return to the district or evades capture by the local nets.

It will be seen that whereas in 1924, 1925, and 1926, 4-zoned 4-ringed herrings were appreciably more numerous than the 3-zoned 3-ringed ones, in 1927 the reverse was the case, for in a sample taken on November 1st, 1927, at Brighton, 70% consisted of year-class 1925. The abundance of herrings of this particular year-class during the winter of 1927 is an interesting observation, for the same phenomenon was observed at Plymouth.

Length for Age.

In view of the importance of the 3-zoned and 4-zoned fishes, the average length and individual variation of individuals in these two age-groups are given below :—

Age.	Date.	Port of Landing.	No. of fishes in each of the following 7 length groups (cm.). 20	21	22	23	24	25	26	Total No.	Average length. cm.	Year. class.
3-zoned 3-ringed	Dec. 9th 1924	Plymouth*	–	2	23	8	1	–	–	34	22·7	1922
	Oct. 19th, 1925	Brighton	–	8	5	1	–	–	1	15	22·3	1923
	Nov. 10th, 1925	Brighton	–	3	5	2	2	–	–	12	22·75	1923
	Dec. 1st, 1925	Brighton	–	11	12	7	3	–	–	33	22·6	1923
	Nov. 1st, 1926	Brighton	–	4	9	7	2	–	–	22	22·8	1924
	Nov. 4th, 1926	Brighton	–	4	13	6	1	–	–	24	22·7	1924
	Dec. 2nd, 1926	Brighton	–	3	6	4	–	–	–	13	22·6	1924
	Dec. 10th, 1926	Hastings	–	–	13	5	2	–	–	20	22·95	1924
	Nov. 1st, 1927	Brighton	–	1	15	39	14	1	–	70	23·5	1925
4-zoned 4-ringed	Dec. 9th, 1924	Plymouth*	–	–	6	9	9	–	–	24	23·6	1921
	Oct. 19th, 1925	Brighton	–	8	21	29	10	–	–	68	23·1	1922
	Nov. 10th, 1925	Brighton	1	2	15	29	9	2	2	60	23·4	1922
	Dec. 1st, 1925	Brighton	–	–	9	10	6	1	–	26	23·5	1922
	Nov. 1st, 1926	Brighton	–	–	11	23	16	3	–	53	23·7	1923
	Nov. 4th, 1926	Brighton	–	–	8	23	22	2	–	55	23·8	1923
	Dec. 2nd, 1926	Brighton	–	–	5	30	22	3	–	60	23·9	1923
	Dec. 10th, 1926	Hastings	–	–	1	23	28	6	1	59	24·2	1923
	Nov. 1st, 1927	Brighton	–	–	2	8	3	2	–	15	23·8	1924

* Caught off Newhaven.

It is sufficient at this stage to point out that the average lengths shown above are markedly less than the corresponding values for herrings landed at Plymouth (cf. Ford, **1**, Part III, p. 293).

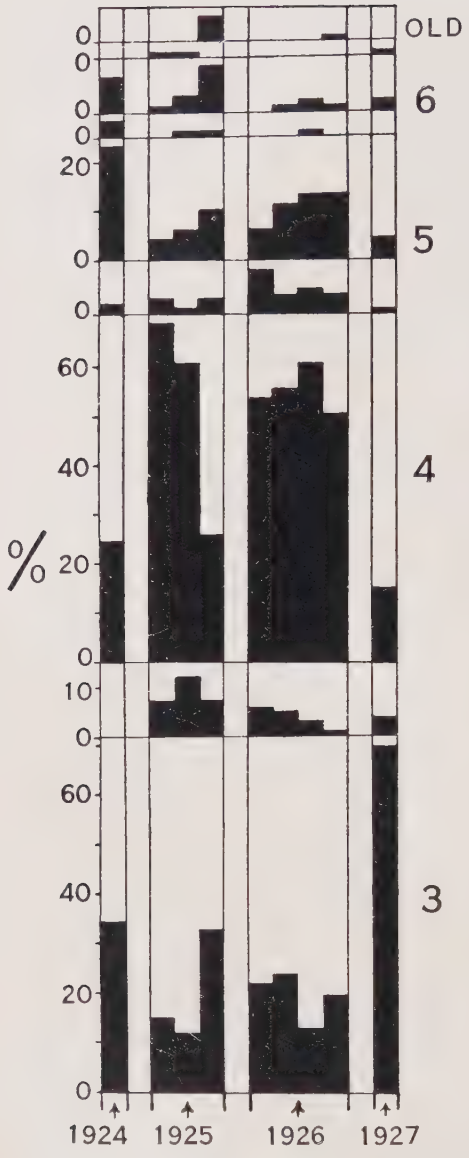

Fig. 1.—Age composition of samples from off Sussex coast.
Samples percentages are shown as small vertical blocks. The age classes are as follows :—

3 . .	3-zoned 3-ringed.
4 . .	4-zoned 4-ringed.
5 . .	5-zoned 5-ringed.
6 . .	6-zoned 6-ringed.
old . .	Zones and rings exceeding 6.

The " interval " classes are 3 or 4, 4 or 5, etc.

Length at Formation of First Winter-ring.

In the consideration of herrings taken in the Sussex district, data on the length (l_1) at the formation of the first winter-ring are of particular interest, for such information bears directly upon the question of the degree to which the herring stock is indigenous to the English Channel or is augmented from the Southern North Sea. Moreover, as already emphasized in previous reports, precise knowledge of the magnitude and variation of l_1 is essential if reliable comparisons of growth are to be made. In Tables III and IV on pages 40, 41, values of l_1 for 3-zoned 3-ringed fishes and 4-zoned 4-ringed fishes are given. The variation, not only from individual to individual, but from sample to sample, is seen to be large in both series. Under such circumstances there appears little justification for attaching great significance to the absolute value of any form of average.

We will examine the data for the 4-zoned 4-ringed fishes. It is evident that the dispersion of the variates over the total range of variation in l_1 differs appreciably from season to season. The samples of 1925 are distinct from those of other years in that they contain a high proportion of herrings with l_1 say from 7 cm. to 9 cm. Now it will be recalled that Hodgson (**2**, p. 16) recognises a "Southern North Sea Type" of

herring (l_1=8 cm.), which he regards as distinct from "Channel" herrings (l_1=12 cm.). In January, 1926, from his study of the scales of herrings landed at Boulogne (*vide* Hodgson, **3**, p. 342), Hodgson concluded that North Sea fish of his Southern Type were spawning along with Channel fish at that time. Under this hypothesis of two distinct types of herrings in the eastern section of the English Channel, it is conceivable that, periodically, Southern North Sea Type herrings may visit the English side of the Channel as well as the French. Such, for instance, would account for the high proportion of fish with l_1 from 7 cm. to 9 cm., in the above Sussex samples during the winter of 1925. Possibly, in other years, this phenomenon is not so marked in extent. A yearly variation in the proportions of the two types would also account for the seasonal differences in dispersion of the variates over the total range in l_1 among the samples taken. This question will, however, receive further attention at a later stage.

Growth subsequent to Formation of First Winter-ring.

In Part I (Ford, **1**, p. 249) it was shown that the data on the growth of 4-zoned 4-ringed fishes caught off the Sussex coast during the seasons 1924 to 1926 could be summarised in the form of five mathematical equations :—

$$l_2 = \cdot 59 l_1 + 11 \cdot 70 \quad \ldots\ldots\ldots \quad (1)$$
$$l_3 = \cdot 504 l_2 + 12 \cdot 80 \quad \ldots\ldots\ldots \quad (2)$$
$$l_4 = \cdot 774 l_3 + 6 \cdot 71 \quad \ldots\ldots\ldots \quad (3)$$
$$l_3 = \cdot 277 l_1 + 18 \cdot 92 \quad \ldots\ldots\ldots \quad (4)$$
$$l_4 = \cdot 221 l_1 + 21 \cdot 28 \quad \ldots\ldots\ldots \quad (5)$$

An illustration was also given of the way these equations might be used to compare the growth of the Sussex fishes with that of fishes of a similar age from a different locality. In the present instance, they will be utilised to compare the data with the growth-characters of Hodgson's "Southern North Sea Type." In **2**, page 16, Hodgson shows diagrammatically the size at each year, which is :—

		cm.	
l_1	l_2	l_3	l_4
8	16	20–21	23

Using equation (1) above, we find the value of l_2 for l_1 of 8 cm. :—

$$l_2 = \cdot 59 l_1 + 11 \cdot 70 \quad \ldots\ldots\ldots \quad (1)$$
$$= \cdot 59(8) + 11 \cdot 70 \quad \ldots\ldots\ldots \quad (2)$$
$$= 16 \cdot 4 \text{ cm. (compare with Hodgson's } l_2 = 16 \text{ cm.).}$$

Using equation (4) above, we find the value of l_3 for l_1 of 8 cm. :—

$$l_3 = \cdot 277 l_1 + 18 \cdot 92 \ldots\ldots\ldots \quad (4)$$
$$= \cdot 277(8) + 18 \cdot 92$$
$$= 21 \cdot 1 \text{ cm. (compare with Hodgson's } l_3 = 20\text{–}21 \text{ cm.).}$$

Using equation (5) above, we find the value of l_4 for l_1 of 8 cm. :—

$$l_4 = \cdot 221 l_1 + 21 \cdot 28 \ldots\ldots\ldots (5)$$
$$= \cdot 221(8) + 21 \cdot 28$$
$$= 23 \cdot 0 \text{ (compare with Hodgson's } l_4 = 23 \text{ cm.).}$$

These results are sufficiently in accord to say that fishes with $l_1 = 8$ cm. caught off the Sussex coast are remarkably similar in growth to those on which Hodgson based his "Southern North Sea Type."

Let us now consider Hodgson's "Channel Type." A total of 36 4-zoned fishes of length 24 cm. examined by him from Brighton on January 4th, 1924, was found to show an average l_1 of 12·34 cm. Using equation (5) above, we find the value of l_4 for l_1 of 12·34 cm. :—

$$l_4 = \cdot 221 l_1 + 21 \cdot 28 \ldots\ldots\ldots (5)$$
$$= \cdot 221(12 \cdot 34) + 21 \cdot 28$$
$$= 24 \cdot 0 \text{ cm. (compare with Hodgson's } l_4 = 24 \cdot 0 \text{ cm.).}$$

This provides reason for arguing that fishes with l_1 about 12 cm. caught off the Sussex coast resemble those of the "Channel Type" of Hodgson. Thus both Southern Northern Sea Type and Channel Type are satisfied by the same growth equations. In other words, so far as growth is concerned, the initial difference between the values of l_1 is, of itself, sufficient to account for the subsequent differences between the values of l_2, l_3, and l_4 in the two types. Expressing this in another way, it may be said that the particular growth conditions which induce 8 cm. whitebait to develop into 4-zoned 4-ringed fishes of the Southern North Sea Type would induce 12·35 cm. whitebait to develop into 4-zoned 4-ringed fishes of the Channel Type; there is no necessity to assume any difference between growth conditions.

Movements of Shoals.

It is convenient to discuss the movements of the shoals by commencing the migratory cycle with the fish on the local grounds in the winter. We have seen that, here, they are "full" fishes approaching maturity. We may, therefore, assume that they will eventually move off to spawn. The observations of Wallace (**5**) and Hodgson (**3**) indicate a spawning region in the neighbourhood of Cap d'Antifer, this locality being not unduly remote from the Sussex coast. Fishes actually spawning were obtained by

Hodgson (3) in January, 1926. After spawning, however, facts are less clear. If we follow le Gall (**4**) we shall now draw a distinction between the Channel Type and the Southern North Sea Type of fish ; we shall contend that the latter retire into the North Sea while the former remain within the English Channel. Regarding this phase, some interest is attached to a sample of fishes caught off Brighton on May 22nd, 1926. Of a total of 65 there were 32 showing 5-zones and 4-rings to the scale. These 32 individuals, then, had obviously been 4-zoned 4-ringed fishes in the winter of 1925, and at the time of capture had commenced their 5th summer zone. In length they varied from 22 cm. to 25 cm, about a mean of 23·9 cm., and their values of l_2, l_3, and l_4 closely approximated to those of the Southern North Sea Type. Thus, while we may freely admit the possibility of an interchange of fish between the North Sea and the English Channel, as le Gall suggests, we must also admit that fishes of the Southern North Sea Type of growth can and do remain within the Channel after spawning.

We have now to consider the nature of the shoals which arrive off the coast of Sussex in the winter. To what extent are they composed of stock which had previously visited the area, and from whence comes any new stock ? We have seen that each season, the bulk of the fishes caught are either 3-zoned 3-ringed or 4-zoned 4-ringed individuals. Thus, the 4-zoned 4-ringed fish do not subsequently return, or at least, are not captured. The 3-zoned 3-ringed ones, may, however, do so in the next year constituting the 4-zoned 4-ringed fishes of the new season. In addition, there must certainly be an important influx of new stock. It is possible that 4-zoned 4-ringed fishes which have never previously visited the area may arrive, conceivably in part from the North Sea, while undoubtedly 3-zoned 3-ringed individuals approaching first maturity will make their appearance for the first time.

Racial Considerations.

As stated in Parts I and II, the methods adopted in the present series of studies enable the worker to investigate growth and migrations without thought of " races " or " racial composition " ; at any rate, in the initial stages. Probably no better illustration could be given of the great practical difficulties to be faced by an investigator who sets out to determine the races represented, than that afforded by the situation in the area under consideration. Here, in brief, are the facts as they are known at present :—

(A) Off the Sussex coast during the winter.

There is a mixed assemblage of " full " fishes which, judging by the values of l_1 deduced from scale measurements, had grown from " whitebait " varying from 5 cm. to 17 cm. in length. There is no uniformity from

sample to sample or from season to season as regards the proportions of the fishes from the different whitebait; sometimes those derived from small whitebait are the more numerous, at other times, those derived from the larger.

(B) On the spawning-ground in the neighbourhood of Cap d'Antifer.

Here, again, there is a mixed assemblage of fishes actually spawning together (Hodgson, **3**). The scale-characters of the spawners are similar to those of the fishes mentioned under (A) above. The larvæ resulting from this spawning may or may not be direct crosses between fishes with small l_1 and those with large l_1. The larvæ themselves may be transported by water movements through the Straits of Dover into the North Sea, and thence to the Thames Estuary where they enter into the composition of the shoals of whitebait along with young herrings from the North Sea itself (Wallace, **5**, p. 7).

(C) Off the Sussex coast during the summer.

Shoals of herrings comparable in growth with those of (A) and (B) above may be met with, still providing evidence of mixture.

In view of these facts it would seem essential that in accumulating statistical material for racial analysis, the age, total length, magnitude of l_1 and stage of maturity would all have to be taken into account. Furthermore, if the "race" data are to be statistically reliable, the number of individuals in each statistical class must be fairly large. This means that the original samples of the mixed catch, taken at random, must be very large. An instance may be given from present records. A random sample of 100 fishes taken off Brighton on November 10th, 1925, included 60 of age 4-zone 4-rings. Of these 60, there were 29 having a total length of 23 cm. The values of l_1 for these 29 individuals were :—

l_1 (cm.).					
7·5	8·5	9·5	10·5	11·5	12·5
2	12	8	4	–	3

Thus, if we wished to obtain reliable data (e.g. on Average No. of Vertebræ or No. of Keeled Scales) concerning 4-zoned 4-ringed fishes of length 23 cm., for different values of l_1, the original random sample would need to be many times larger than the one actually taken. To complete the amount of additional routine work occasioned by thus largely increasing the size of the random sample, especially when sampling itself must be frequent, would be beyond the capacity of a single investigator.

Herrings caught in the Great West Bay.

The herrings landed at Brixham during the winter form an interesting study, but care must be taken to ascertain the particular locality from which the fishes have been landed. In some seasons the shoals upon which the Plymouth steam fishery is being concentrated are located well up Channel off Start Point and a certain number of East Country steamers may elect temporarily to use Brixham as their port of landing. Apart from this, however, drift and standing nets are every year worked still farther to the eastward in the Great West Bay, and it is concerning these fish that information is given below. Between November, 1925, and January, 1927, eight samples were sent to Plymouth from Brixham, where they were submitted to the usual routine examination.

Condition of Gonads (Roes and Milts).

The following is a summary of the data on the degree of maturity of the gonads :—

		No. of Fishes in each of the 4 following classes :—				
		Immature.	Full.	Ripe.	Spent.	
		Hjort's	Hjort's	Hjort's	Hjort's	Total No.
Sample.	Date.	Stage I.	Stages IV & V.	Stage VI.	Stage VII.	of Fishes.
5.	Oct. 27th, 1926	–	109	1	–	110
1.	Nov. 9th, 1925	–	75	2	2	79
2.	Nov. 26th, 1925	3	114	3	–	120
6.	Nov. 23rd, 1926	–	116	2	–	118
3.	Dec. 16th, 1925	–	56	34	5	95
7.	Dec. 14th, 1926	–	113	4	3	120
4.	Jan. 4th, 1926	–	9	12	43	64
8.	Jan. 20th, 1927	–	17	93	–	110

These samples indicate that we have to deal with December and January spawning fishes. Sample 8, of which about 90% were fully mature ♂ and ♀ fishes, was from a total catch of 20 crans made by a motor-drifter off Exmouth, so that it is reasonable to suspect that actual spawning occurred at no great distance from this locality. As in the case of the Sussex herrings, the youngest fishes (3-zoned 3-ringed) gave evidence that they would spawn in their third winter of life in the scaled condition.

Average Length.

It will be seen from the values of Q_1, Q_2, and Q_3 given in Table V on page 41, that there are appreciable differences in length distribution between samples. Thus, on November 26th, 1925, the middle 50% (Q_3–Q_1) included fishes of the 22 cm., 23 cm., and 24 cm. length groups,

whereas on January 4th, 1926, it comprised those of the 25 cm., 26 cm., and 27 cm. groups. Sample 3, taken on December 16th, 1925, on the other hand, is bimodal as regards length. No very useful purpose, therefore, is served by conducting a more detailed analysis of the raw length data as they stand. There is, however, one point of interest which was referred to in Part III (**1**, p. 287). It was there shown that in the Plymouth samples there was a tendency for the average length to be lower towards the eastwards. (i.e. from Plymouth towards Start Point). The present series of samples was taken from catches made in waters still farther to the eastward, and it will be observed that there is a further depression in the lower quartile length (Q_1). That is to say, a larger proportion of smaller fishes is likely to be landed from the Great West Bay than from the area covered by the Plymouth fishery. It is thus possible that in the intermediate waters to the eastward of Plymouth some overlap of fish-population may occur.

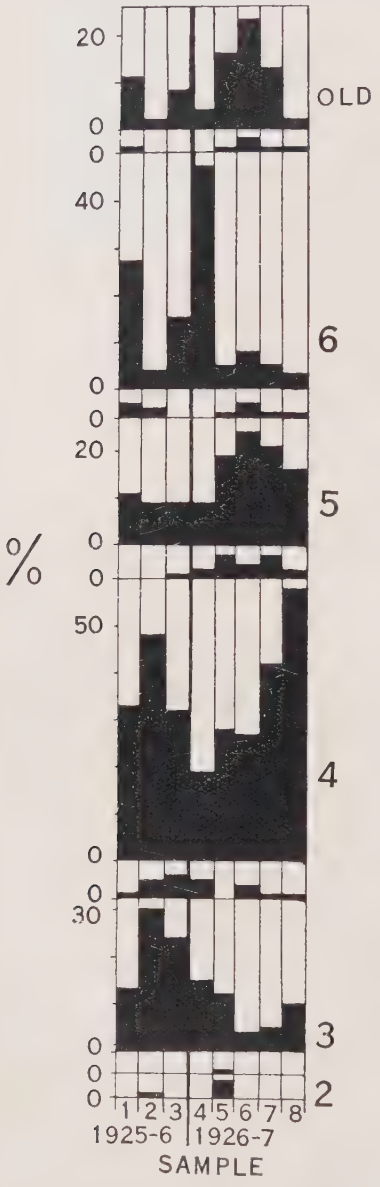

FIG. 2.—Age composition of samples from Great West Bay.
Details as in Fig. 1 (page 28).

Age Composition of Samples.

Estimates of age from scale-readings, expressed in the form of percentages, are given in Table VI on page 42, and recorded graphically in Fig. 2.

In the first place it will be noted that the 4-zoned 4-ringed class was always well represented; in 7 of the total of 8 samples it was actually the dominant constituent. The samples of the season 1925–26 also showed an appreciable percentage of 3-zoned 3-ringed fishes. In this heavy proportion of young fishes, then, the situation resembles that experienced off the Sussex coast (*vide* p. 27).

Unlike the Brighton and Hastings samples, however, the present ones

include an appreciable percentage of individuals older than 4-zones 4-rings. Of these older individuals, those of the year-class 1920, as 6-zoned 6-ringed fishes, were important during the season 1925–26, and again as 7-zoned 7-ringed fishes in the following season, 1926–27. On the other hand, fishes of the 1921 class were scarce either as 5-zoned 5-ringed in 1925–26 or as 6-zoned 6-ringed in 1926–27. In these respects, the situation is reminiscent of Plymouth during the corresponding period (*vide* Ford, **1**, Part III, p. 289).

The contribution each season made by the year-classes concerned is shown in convenient summary form below :—

Season.	Date of sample.	Percentage of sample in each of 5 year-classes. 1920		1921		1922		1923		1924	
1925–26	Nov. 9	26·6	as 6-zoned 6-ringed fishes.	11·4	as 5-zoned 5-ringed fishes.	32·9	as 4-zoned 4-ringed fishes.	12·7	as 3-zoned 3-ringed fishes.	—	
	Nov. 26	4·0		9·0		48·0		30·0		—	
	Dec. 16	15·3		9·4		31·8		28·2		—	
	Jan. 4	47·2		9·4		18·9		15·1		—	
1926–27	Oct. 27	11·0	as 7-zoned 7-ringed fishes.	5·0	as 6-zoned 6-ringed fishes.	19·0	as 5-zoned 5-ringed fishes.	28·0	as 4 zoned 4-ringed fishes.	12·0	as 3-zoned 3-ringed fishes.
	Nov. 23	20·0		8·0		24·0		27·0		4·0	
	Dec. 14	10·0		5·0		21·0		42·0		5·0	
	Jan. 20	2·0		3·0		19·0		58·0		10·0	

In Part III (Ford, **1**, p. 291), in summarising the evidence to be drawn from the results of age-estimations on Plymouth fishes during the season 1926–27, the following was stated : " . . . that the 1920 class showed definite signs of a decline in intensity, and that the 1921 class gave no signs that it would ever become important, while of the younger classes, that of 1923 was the most promising."

An examination of the data summarised in the table above shows that this might equally well be written concerning the samples from the Great West Bay.

Length for Age.

Fishes of the same age differ so much in total length that little practical significance can be attached to the average length calculated from the lumped sample data throughout one season for a given year-class. Interesting evidence, however, is to be obtained from the data for individual samples :—

3-zoned 3-ringed Fishes.

Season.	Date.	No. of Fishes in each of 8 Length groups (cm.). 20	21	22	23	24	25	26	27	Total No.	Year-class.
1925–26	Nov. 9	–	–	1	1	1	3	2	2	10	
	Nov. 26	2	2	12	8	4	1	1	–	30	1923
	Dec. 16	–	4	7	10	2	1	–	–	24	
	Jan. 4	–	–	3	–	–	1	4	–	8	
1926–27	Oct. 27	–	–	3	4	1	1	2	1	12	
	Nov. 26	–	–	–	–	–	2	1	1	4	1924
	Dec. 16	–	–	1	1	–	–	3	–	5	
	Jan. 20	–	1	2	4	1	2	–	–	10	

It is seen that there is a tendency for the individuals to group themselves in two parts of the total range in length, viz. in the 22 and 23 cm. groups and again in the 25 and 26 cm. groups. This is instructive, for if we turn to the Sussex samples (p. 27) we see that the 3-zoned 3-ringed fishes largely fall into the 22 cm. and 23 cm. length groups; on the other hand, if we refer to the Plymouth samples of 1926–27 (Ford, **1**, Part III, p. 293) we see that the 3-zoned 3-ringed fishes largely fall into the 25 and 26 cm. length groups.

4-zoned 4-ringed Fishes.

Season.	Date.	No. of Fishes in each of 9 Length groups (cm.). 21	22	23	24	25	26	27	28	29	Total No.	Year-class.
	Nov. 9	–	2	1	5	4	8	5	–	1	26	
1925–26	Nov. 26	1	11	15	13	4	4	–	–	–	48	1922
	Dec. 16	–	11	5	3	4	3	1	–	–	27	
	Jan. 4	–	–	1	2	4	2	1	–	–	10	
	Oct. 27	–	1	1	20	5	1	–	–	–	28	
1926–27	Nov. 26	–	–	1	13	5	7	1	–	–	27	1923
	Dec. 16	–	–	8	16	14	3	1	–	–	42	
	Jan. 20	–	2	13	33	9	1	–	–	–	58	

In this age-group, fishes group themselves in different parts of the total length range in different samples. Here again it is interesting to compare the data with those from Sussex and Plymouth. In the Brixham sample of November 26th, 1925, of a total of 48 individuals, 39 fall into the 22, 23, and 24 cm. length groups. This compares favourably with a sample of sixty 4-zoned 4-ringed fishes taken off Brighton on November 10th, 1925, of which 53 fall into the same length groups. In contrast with this, it is to be noted that during the season 1925–26 at Plymouth, 4-zoned 4-ringed fishes grouped themselves largely in the 25, 26, and 27 cm. groups, whereas here in the Great West Bay samples, fishes of a similar age exceeding 26 cm. in length are few in number.

5-zoned 5-ringed Fishes.

As already stated above, fishes of this age (1921 year-class) were relatively unimportant during the season 1925–26. In the following season, however, when the members of the 1922 year-class had become 5-zoned 5-ringed fishes, the proportion was appreciable. The length-distribution was as follows:—

Season.	Date.	No. of Fishes in each of 6 Length groups (cm.). 23	24	25	26	27	28	Total No.	Year-class.
	Oct. 27	3	6	6	1	3	–	19	
1926–27	Nov. 26	–	2	12	3	5	2	24	1922
	Dec. 16	1	3	9	5	3	–	21	
	Jan. 20	2	6	9	2	–	–	19	

Compared with the Plymouth fishes of the same year-class during the same season (*vide* Ford, **1**, Part III, p. 293) the above are distributed over a lower part of the length-range.

6-zoned 6-ringed Fishes.

Members of the 1920 year-class as 6-zoned 6-ringed fishes were of considerable importance in three of the four samples taken during the season of 1925–26. Data on length are as follows :—

Season.	Date.	No. of Fishes in each of 7 Length groups (cm.). 25	26	27	28	29	30	31	Total No.	Year-class.
	Nov. 9	1	3	10	3	2	–	1	21	
1925–26	Nov. 26	–	1	3	–	–	–	–	4	1920
	Dec. 16	2	5	4	1	1	–	–	13	
	Jan. 4	3	6	5	7	4	–	–	25	

The fishes of the 1920 year-class caught during the season 1925–26 at Plymouth (*vide* Ford, **1**, Part III, p. 293) were largely grouped in the 26, 27, 28, and 29 cm. length groups, and of an average length of 27·9 cm.

7-zoned 7-ringed Fishes.

During the season 1926–27, a fair proportion of the 1920 class, now as 7-zoned 7-ringed individuals, was present in the samples :—

Season.	Date.	No. of Fishes in each of 4 Length groups (cm.). 25	26	27	28	Total No.	Year-class.
	Oct. 27	–	1	6	4	11	
1926–27	Nov. 26	–	8	10	2	20	1920
	Dec. 16	3	7	–	–	10	
	Jan. 20	–	2	–	–	2	

The above are certainly distributed over a lower part of the length range than corresponding fishes landed at Plymouth.

From the foregoing considerations of length for age it seems permissible to draw two conclusions concerning the herrings landed from the Great West Bay :—

(*a*) Of the fishes of the younger age-groups (3-zoned 3-ringed and 4-zoned 4-ringed) many are of a length similar to that for fishes of corresponding age caught off the Sussex coast.

(*b*) Herrings of the older age-groups (5-zoned 5-ringed and older) are generally distributed over a lower part of the total length range than similar aged fishes taken in Plymouth waters during the same period.

Length at Formation of First Winter-ring (l_1).

In view of the relative importance in the catches of 4-zoned 4-ringed fishes, the lengths l_1, l_2, and l_3 have been calculated from scale-measurements. The data on l_1 for each sample are as follows :—

4-zoned 4-ringed Fishes.

Season.	Date	L1. Central values of 12 classes (cm.). 6·5	7·5	8·5	9·5	10·5	11·5	12·5	13·5	14·5	15·5	16·5	17·5	Total No. of fishes.	Year-class.
1925–26	Nov. 9	–	2	3	1	4	1	2	6	2	2	1	1	25	
	Nov. 26	2	5	13	10	4	4	–	2	1	–	–	–	41	1922
	Dec. 16	1	2	9	1	2	1	1	3	1	–	–	–	21	
	Jan. 4	–	–	2	1	1	3	1	1	1	–	–	–	10	
	Oct. 27	–	2	5	3	2	2	3	5	4	1	–	–	27	
1926–27	Nov. 26	–	–	2	1	5	2	3	3	5	5	–	1	27	1923
	Dec. 16	–	1	–	3	7	2	7	3	6	7	2	–	38	
	Jan. 20	–	–	2	4	10	5	7	6	8	6	4	1	53	

Thus, as has been seen at Brighton and Plymouth, the value of l_1 for fishes in the Great West Bay varies over a considerable range. The sample of November 26th, 1925, is interesting in that there was an appreciable number of fishes with l_1 from 7·5 to 9·5 cm. This reminds us of the situation at Brighton. More frequently, however, l_1 is comparatively large, often exceeding 12·5 cm., and in this respect, the samples are in closer agreement with those of similar-aged fishes landed at Plymouth.

Average Number of Vertebræ.

Data on the number of vertebræ for herrings of the samples under consideration have already been given in Part II (Ford, **1**). If we refer to Fig. 1 on page 274 of that paper, we see that the average number of vertebræ for these Great West Bay fishes is intermediate between that for Plymouth and that for Sussex herrings. This fact is instructive in view of the results of age and growth comparisons described above.

From the results discussed in the preceding pages, then, we see that the herrings landed from the Great West Bay during the winter present an interesting problem for further study. Efforts must be directed towards an understanding of why, on the one hand, there is a measure of similarity to the Sussex fish, and, on the other, to those landed at Plymouth. By a detailed systematic sampling it should be possible to arrive at a fuller knowledge of the migratory cycles of the herrings frequenting the English Channel generally, and, incidentally, therefore, to throw light on these movements as they concern the Plymouth shoals in particular.

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TABLE I.

Herrings caught off Sussex Coast.

Sample No.	Date.	Port of Landing.	Total No. of Fishes.	Length Distribution (cm.). Lower Limit.	Lower Quartile Q_1.	Median Q_2.	Upper Quartile Q_3.	Upper Limit.
	1924							
1.	Dec. 9	Plymouth*	161	21·5	22·6	23·6	24·7	26·5
	1925							
2.	Oct. 19	Brighton	128	20·5	22·1	23·0	23·8	26·5
3.	Nov. 10	,,	100	20·5	22·8	23·5	24·3	27·5
4.	Dec. 1	,,	118	21·5	22·4	23·4	24·7	29·5
	1926							
5.	Nov. 1	Brighton	120	21·5	22·9	23·5	24·2	26·5
6.	Nov. 4	,,	100	21·5	22·9	23·6	24·3	25·5
7.	Dec. 2	,,	100	21·5	23·2	23·9	24·6	25·5
8.	Dec. 10	Hastings	120	22·5	23·2	24·0	24·6	26·5
	1927							
9.	Nov. 1	Brighton	102	21·5	23·1	23·9	24·6	25·5

* This sample was from a steamer landing at Plymouth. Nets were shot off Newhaven on the journey westward to Plymouth from Lowestoft.

TABLE II.

Herrings caught off Sussex Coast.

PERCENTAGE AGE COMPOSITION (ZONES AND RINGS).

Sample No.	Date.	3	3–4	4	4–5	5	5–6	6	6–old	Older than 6.	Total No. of Fish.
	1924										
1.	Dec. 9	34	–	24	2	23	3	7	–	–	100
	1925										
2.	Oct. 19	15	7	68	3	4	–	1	1	–	100
3.	Nov. 10	12	12	60	1	6	1	3	1	–	100
4.	Dec. 1	33	7	26	3	10	1	9	–	5	100
	1926										
5.	Nov. 1	22	6	53	9	6	–	–	–	–	100
6.	Nov. 4	24	5	55	4	11	–	1	–	–	100
7.	Dec. 2	13	3	60	5	13	1	2	–	3	100
8.	Dec. 10	20	1	59	4	13	–	1	1	–	100
	1927										
9.	Nov. 1	70	5	15	1	4	–	2	–	–	100

TABLE III.

Herrings caught off Sussex Coast.

3-zoned 3-ringed Fishes.

Sample.	Date.	L_1. Central Valves of 10 Length classes (cm.). 7·5	8·5	9·5	10·5	11·5	12·5	13·5	14·5	15·5	16·5
	1925										
2.	Oct. 19	–	1	–	3	–	3	2	5	–	–
3.	Nov. 10	–	–	1	–	2	3	3	2	–	1
4.	Dec. 1	–	–	2	3	10	5	4	2	4	1
	1926										
5.	Nov. 1	–	–	–	2	6	4	2	3	3	–
6.	Nov. 4	–	–	3	3	5	6	4	1	2	–
7.	Dec. 2	1	1	1	1	4	3	1	–	1	–
8.	Dec. 10	–	–	2	2	3	3	1	3	4	1

TABLE IV.

Herrings caught off Sussex Coast.

4-zoned 4-ringed fishes.

Sample.	Date.	L_1. Central Valves of 13 Length classes (cm.). 5·5	6·5	7·5	8·5	9·5	10·5	11·5	12·5	13·5	14·5	15·5	16·5	17·5
	1924													
1.	Dec. 9	–	–	2	1	5	4	5	6	1	–	–	–	–
	1925													
2.	Oct. 19	1	1	10	24	9	9	7	3	2	–	–	–	
3.	Nov. 10	–	1	6	22	13	8	2	5	–	–	1		
4.	Dec. 1	–	1	2	7	5	–	2	5	1	–	–	–	–
	1926													
5.	Nov. 1	–	–	3	5	5	9	15	4	3	1	2	–	–
6.	Nov. 4			1	3	4	12	15	5	5	–	–	–	
7.	Dec. 2	–	–	–	4	6	11	11	8	6	6	5	1	–
8.	Dec. 10	–	–	–	3	7	2	12	11	8	5	3	2	1

TABLE V.

Herrings caught in the Great West Bay.

Sample No.	Date.	Total No. of Fishes.	Length Distribution (cm.). Lower Limit.	Lower Quartile Q_1.	Median Q_2.	Upper Quartile Q_3.	Upper Limit.
	1925						
1.	Nov. 9	79	22·5	25·8	27·0	28·0	31·5
2.	Nov. 26	120	20·5	22·7	23·7	24·9	28·5
3.	Dec. 16	94	21·5	22·75	24·0	26·4	29·5
	1926						
4.	Jan. 4	64	22·5	25·1	26·6	28·1	29·5
5.	Oct. 27	110	21·5	24·2	25·1	27·1	29·5
6.	Nov. 23	118	23·5	25·3	26·2	27·2	28·5
7.	Dec. 14	120	22·5	24·5	25·4	26·1	27·5
	1927						
8.	Jan. 20	110	21·5	23·9	24·6	25·25	26·5

TABLE VI

Herrings caught in the Great West Bay.

PERCENTAGE AGE COMPOSITION (ZONES AND RINGS).

Sample No.	Date.	2	2–3	3	3–4	4	4–5	5	5–6	6	6–old	Older than 6	Total No. of Fish.
	1925												
1.	Nov. 9	–	–	12·7	1·3	32·9	–	11·4	2·5	26·6	1·3	11·4	79
2.	Nov. 26	1	–	30	4	48	–	9	2	4	–	2	100
3.	Dec. 16	–	–	28·2	5·9	31·8	1·2	9·4	–	15·3	–	8·3	85
	1926												
4.	Jan. 4	–	–	15·1	3·8	18·9	1·9	9·4	–	47·2	–	3·8	53
5.	Oct. 27	4	1	12	–	28	5	19	1	5	3	16	100
6.	Nov. 23	–	–	4	3	27	3	24	3	8	2	23	100
7.	Dec. 14	–	–	5	1	42	5	21	1	5	2	13	100
	1927												
8.	Jan. 20	–	–	10	1	58	2	19	1	3	–	2	100

Herring Investigations at Plymouth. VII. On the Artificial Fertilisation and Hatching of Herring Eggs under known Conditions of Salinity, with some Observations on the Specific Gravity of the Larvæ.

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Introduction.

It has previously been shown (Ford, **1**, p. 284) that herrings with fully ripened roes or milts form a considerable proportion of the landings by commercial drifters at Plymouth during December and January. Although naturally-deposited spawn has rarely been obtained from the sea-bottom in the district, the fact that newly-hatched larvæ occur in abundance provides evidence that actual spawning occurs locally. It has also been shown that from the end of September onwards, ripe fishes may be taken in stop-nets in Plymouth Sound, and even in sprat-seines in the estuarine waters of the River Tamar. A number of interesting and important questions is suggested by these observations. For example, do the ripe herrings which frequent the River Tamar actually spawn there, and if so, are they morphologically identical with those which spawn at sea, or are they of a different character ? Would eggs deposited in the river be successfully fertilised and able to endure the periodic freshening of the water ? Are the morphological characters of the offspring in any way dependent upon the environmental conditions under which they are developed ?

It is a comparatively simple process to express the eggs from a recently-dead ripe female on to glass plates, and then to fertilise them with the milt from a ripe male. The fertilised eggs develop quite normally in sea-water and give a good yield of apparently healthy and active larvæ. Unfortunately, however, it seems impossible at present to rear these larvæ beyond the stage at which the yolk-sac is absorbed. Thus, while we can readily obtain a batch of larvæ from the artificial crossing of parents of known character, we cannot, as yet, rear the young to the stage at which they exhibit the adult characters used to define the parents. It will be realised that this fact is a serious hindrance to progress along

the lines of investigation under consideration, and it is to be hoped that some worker will soon be able to devote time to discover how successfully to rear herring larvæ. The problem will need undivided attention ; it is not one likely to be solved as an incidental to other investigations.

There are, however, important initial points which can be cleared up by experiments in artificial fertilisations alone. During the winter of 1928–29 some preliminary tests were made, having as their object the determination of the effects of changing salinity as one leading environmental factor. The nature of the experiments and the results obtained are discussed below.

Experiment A.

During the evening of January 14th, 1929, eggs from a ripe female herring 27·5 cm. in length were expressed on to four glass plates and fertilised by the milt of a ripe male 27·3 cm. in length. Laboratory tank-room sea-water was used throughout the fertilisations, at a temperature of 7·5° C. On the morning of January 15th the plates with the developing eggs were transferred, one to each of the following tanks :—

Tank 1. 8000 cc. Laboratory tank-room sea-water.
Tank 2. 4000 cc. ,, ,, +4000 cc. fresh-water from tap.
Tank 3. 2000 cc. ,, ,, +6000 cc. ,, ,,
Tank 4. 1000 cc. ,, ,, +7000 cc. ,, ,,

The salinities of these tanks, determined by titration against silver nitrate solution according to the method recommended by Harvey (**2**, p. 37), were as follows :—

Tank 1.	37·8
Tank 2.	18·8
Tank 3.	9·34
Tank 4.	4·75

Rough sketches of the disposition of the eggs on each plate were made, indicating unfertilised eggs. These sketches provided a means of ascertaining at a glance if any eggs died subsequent to transference to the test tanks. Each tank was aerated continuously throughout the experiment. On January 25th, larvæ began to hatch out in Tanks 1 and 2, and, on the following day, in the remaining Tanks 3 and 4. No eggs had apparently died during the experiment. Within the next two or three days the whole of the eggs in Tanks 1 and 2 hatched out, but in Tanks 3 and 4, particularly the latter, many of the larvæ appeared rather weakly, for although they broke through the egg-envelope, they were unable to wriggle entirely free from it. On February 4th, ten days after the first larvæ were hatched, a few individuals still remained alive in all four tanks.

There was, however, a greater percentage of survivors in Tanks 1 and 2 than in Tanks 3 and 4.

Thus, eggs fertilised in tank-room sea-water will survive exposure to freshened sea-water of a salinity at least as low as 5, and give rise to living larvæ, some of which will remain alive in that water until the absorption of the yolk has reached an advanced stage.

Experiment B.

On January 22nd an attempt was made to obtain successful fertilisations, not only in sea-water of normal salinity, but in different mixtures of salt and freshwater. A female of 28·5 cm. and a male of 28·3 cm. were used for the experiment and operations conducted in water of from 9°–10° C. The following were the results :—

Plate No.	Water used. Sea-water.	Fresh (tap).	Salinity.	Result.
1	2000 cc.	—	37·8	Successful fertilisation.
2	1000 cc.	1000	19·0	,, ,,
3	250 cc.	1750	4·8	,, ,,
4	125 cc.	1875	2·4	One or two eggs fertilised, remainder unfertilised.
5	—	2000	—	Failure.

Thus, actual fertilisation seems certainly possible in water of salinity of 4·8, and may even be possible in still fresher water down to a salinity of 2·5.

Plates 1, 2, and 3 carrying the successfully fertilised eggs were placed in tanks of water of the following salinities :—

Plate No.	Tank. Sea-water.	Fresh (tap).	Salinity.
1	2000 cc.	—	37·8
2	1000 cc.	1000	19·0
3	250 cc.	1750	4·8

On February 4th larvæ hatched from the eggs on all three plates. That is to say, eggs fertilised in water of salinity as low as 5 will develop in that water and give rise to living larvæ.

Now although the results of these experiments need confirmation and elaboration, they are of immediate local application. If the eggs of herrings taken from the sea are capable not only of being fertilised, but also of undergoing successful incubation in water varying in salinity from 37·8 to 4·8, it is perfectly logical to believe that, so far as salinity is concerned, the fishes experimented with could, if they had been free to choose, have spawned on any suitable ground either outside or

within Plymouth Sound or at places some considerable distance up the rivers Tamar and Lynher, with fair chances of a satisfactory brood of larvæ.

Specific Gravity of Larvæ.

Herring larvæ in an aquarium filled with ordinary sea-water, when not actually swimming, tend to sink at an appreciable rate. During the course of experiments A and B above, the impression was gained that larvæ in diluted sea-water sank more quickly than those in undiluted, and, in consequence, were more often at the bottom of the aquaria than at the surface. It was therefore decided to make some comparisons between larvæ incubated and reared in different strengths of sea-water, regarding their specific gravity. The method was to determine by trial and error the particular one of a series of brines of known strength in which a larva would remain in equilibrium, neither rising nor falling.

The standard brine used was 100 grammes of common salt dissolved in 500 cc. of tap-water, and the following series of test brines was made up at a temperature of 12° C. :—

Test Brine No.	Standard Brine cc.	Tap-water cc.	Actual Strength of Test Brine.
1	50	50	10 grm. NaCl per 100 cc.
2	47·5	52·5	9·5 ,, ,, ,,
3	45	55	9·0 ,, ,, ,,
4	42·5	57·5	8·5 ,, ,, ,,
5	40	60	8·0 ,, ,, ,,
6	37·5	62·5	7·5 ,, ,, ,,
7	35	65	7·0 ,, ,, ,,
8	32·5	67·5	6·5 ,, ,, ,,
9	30	70	6·0 ,, ,, ,,
10	27·5	72·5	5·5 ,, ,, ,,
11	25	75	5·0 ,, ,, ,,
12	22·5	77·5	4·5 ,, ,, ,,
13	20	80	4·0 ,, ,, ,,
14	17·5	82·5	3·5 ,, ,, ,,

The number of larvæ available for experiment was limited, and no opportunity presented itself later to make further fertilisations, so that the results obtained are tentative. Some difficulty, also, was experienced in actual practice, on account of the intermittent swimming of the larvæ in the test brines ; in future tests it might be profitable to employ an anæsthetic.

It soon became evident that the specific gravity of the larva depended upon the amount of unabsorbed yolk in the yolk-sac, newly-hatched

larvæ remaining in equilibrium in much stronger brine than larvæ some 10 days old. In the following table the results are given for tests of larvæ of different ages. The larvæ used were all hatched from eggs fertilised and incubated in sea-water of salinity 37·8 :—

Age of larvæ.	No. of larvæ remaining in equilibrium in following test brines :— 2	2–3*	3	3–4*	4	4–5*	5	5–6*	6	6–7*	7	7–8*	8	8–9*	9	9–10*	10	10–11*	11
6 hours or less after hatching	2	1	1	3	2	1	–	4	–	–	–	–	–	–	–				–
24 hours or less after hatching	–	1	1	1	–	3	1	6	3	3	1	–	–	–	–	–	–	–	–
2nd day after hatching	–	–	–	1	1	1	–	1	–	1	1	1	1	1	1	–	–	–	–
3rd day after hatching	–	–	–	–	–	–	–	1	–	2	1	2	1	1	1	1	–	–	–
4th day after hatching	–	–	–	–	–	–	–	–	–	1	1	–	–	1	1	1	–	–	–
9–10 days after hatching	–	–	–	–	–	–	–	–	–	–	–	1	–	1	1	3	2	–	–
10–12 days after	–	–	–	–	–	–	–	–	–	–	–	1	–	1	1	1	3	1	2

In consequence of this difference of specific gravity due to the quantity of unabsorbed yolk, it will be appreciated that, in attempting to draw comparisons between larvæ fertilised and/or incubated in different strengths of sea-water, it is essential that the larvæ compared should be of similar age and of the same parentage. In the present series, such material was limited, but the results tabulated below are interesting and suggestive although they need confirmation :—

Larvæ from Experiment B (above).

Age of larvæ.	Larvæ hatched from eggs fertilised and incubated in water of following salinity.	No. larvæ remaining in equilibrium in following test brines. 2	2–3	3	3–4	4	4–5	5	5–6	6	6–7	7	7–8	8	8–9	9
Maximum of	37·8	1	2	–	2	1	–	–	2	–	–	–	–	–	–	–
24 hrs. after	19·0	–	–	–	–	–	–	1	1	2	1	–	3	–	1	–
hatching	4·8	–	–	–	–	–	–	–	–	–	–	–	–	–	3	1

Larvæ from Experiment A (above).

Age of larvæ.	Larvæ hatched from eggs fertilised in sea-water of salinity 37·8 but incubated and reared in water of following salinity.	No. larvæ remaining in equilibrium in following test brines :— 7–8	8	8–9	9	9–10	10	10–11	11	11–12	12	12–13	13	13–14
9–10 days	37·8	1	–	1	1	3	2	–	–	–	–	–	–	–
after	19·0	–	–	–	2	1	1	–	–	–		–	–	–
hatching.	4·8	–	–	–	–	–	–	–	–	1	1	–	1	1

* The interval classes 2–3, 3–4, etc., indicate that the larvæ concerned do not remain in equilibrium in any one of the series of brines. Thus, a larvæ entered in Class 2–3 rises in brine 2 and falls in brine 3.

These results suggest that by incubating eggs in freshened water and allowing the newly-hatched larvæ to develop under the same salinity conditions, the specific gravity becomes reduced at a rate dependent upon the degree of freshening of the water.

The phenomenon of changing specific gravity of larvæ, due either to the gradual absorption of yolk during development or to the fact that incubation was carried out in freshened water, or both, would seem to merit attention. Herring larvæ being appreciably heavier than the water in which they live will tend to sink to the sea-bottom unless they persistently swim towards the surface; upward progress will be less easy for newly-hatched larvæ than for older ones on account of their higher specific gravity and their inferior swimming power. Questions relating to horizontal and vertical distribution of herring larvæ at different ages may well be affected by such factors.

In the second place, the differences of specific gravity induced by freshening of the water may conceivably have its effect on the metabolism of the larva, with a resulting morphological reaction. Such would be a highly important matter in all questions relating to racial investigations.

The results of these preliminary experiments, therefore, suggest that a fuller investigation along the lines indicated would be most profitable.

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The Reproductive Organs of the Herring in Relation to Growth.

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With 4 Figures in the Text.

The different organs of an animal do not all grow at one speed. Some develop precociously, and others, like the reproductive system, are delayed for a considerable time in their development, though ultimately they may become very large. In a mature herring about one-fifth of the entire weight consists of reproductive tissues. The different organ-growths are integrated into the growth of the whole body, and one kind of curve will represent both the parts and the whole.

In the herring there are great seasonal changes consequent upon spawning. The weight of the gonads reaches a maximum and then falls abruptly to zero, after which it increases again to the next maximum at the following spawning season. The amplitude of this fluctuation is an increasing one; and, at the suggestion of Dr. J. H. Orton, I have made the following analysis to discover whether a time comes ultimately when the increasing tax of spawning brings about the animal's death. If the successive gonad-maxima go on increasing after the general body-growth has slowed down, this may be the case; on the other hand, if the growth-rate of the gonads is not greater than that of the body in old fishes, it may be assumed confidently that death is due to other causes.

While at Port Erin in 1925 I made a series of weighings and age-determinations which provided data exactly suited to the investigation of this point, on which this paper is based.

Material.

The samples of herrings used fall into two series, one from the Irish Sea within a radius of twenty miles of the Chickens Lighthouse, to the south of the Isle of Man, locally called *Calf Herrings;* the other from inshore shoals off Port Erin bay, known as *Low Herrings*, which spawn slightly earlier. The principal part of this paper deals with the Calf

samples, which were more numerous and extend over the whole spawning season. They were obtained from Scottish steam-drifters at Port St. Mary between August 18th and September 25th, 1925.

Within a few hours of landing the fish were measured and weighed, the gonads removed and weighed also. At the same time scales taken

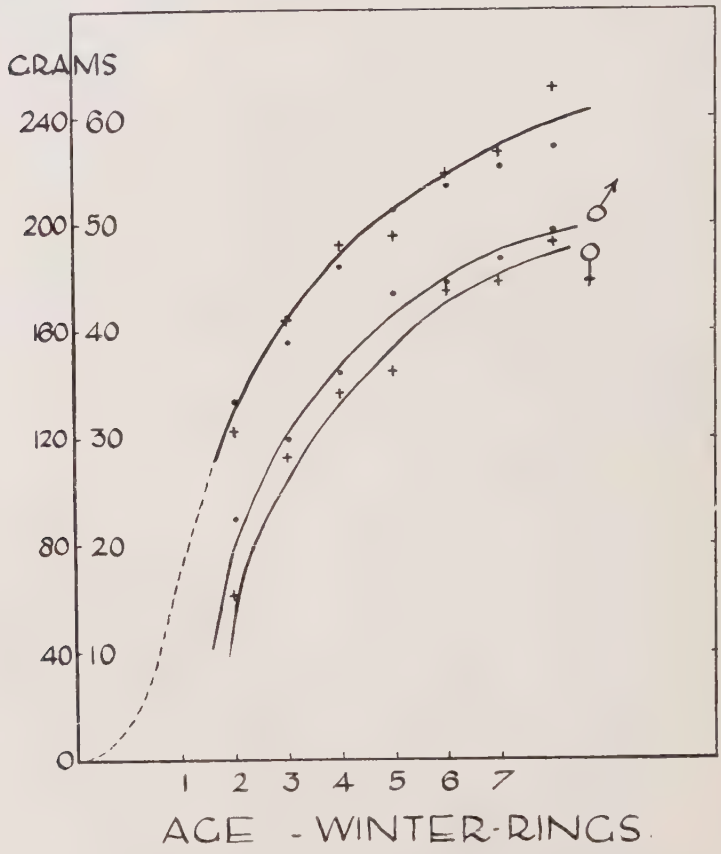

Fig. 1.—Total Body-Weights (upper curve) and Gonad-Weights (lower curves) of Calf herring, plotted against age.
Data for males represented by dots, and for females by crosses.

from each fish were placed in numbered watch-glasses, and from these age-determinations were made. Scales with more than seven dark winter-rings were regarded as unreliable in age-determination, and have been disregarded in curve-fitting.

Fish in other than stages V and VI of maturity could not of course be used, and this, together with the separation of the sexes, reduces the data materially. Tests have been made, however, to show that where

conclusions have been drawn, they are mathematically justified. The fact that the curves are not smooth does depend to some extent upon the numbers available, but also very largely on the natural diversity of different year-classes of herrings from the same shoals. From the numbers of each year-class obtained by sampling it is clear that different years offer different chances of survival at least, and probably also of growth ; complete homogeneity would not be realized, however great the sample might be.

Age-frequency of Calf Herrings.

Year of birth	1918	1919	1920	1921	1922
Frequency	83	83	54	61	80

Subsequent sections refer to the *Calf* samples, unless otherwise stated.

Body-weight.

The rate of growth is at its maximum when the fish is about two years old ; that is, the point of inflexion of the S-shaped growth-curve occurs at this time. Consequently all the material considered here is situated in the upper portion of the curve, where the growth-rate is continually decreasing. This growth-curve is similar to that of autocatalysis, and has been studied by Pearl (**3**). No attempt has been made here at curve-fitting, so that it is not possible to say whether the growth of the two sexes can be represented by a single curve, or whether they form two distinct curves. It appears from Fig. 1 that they are, at any rate, very close together, if not identical. The females attain a greater weight in these samples, and apparently a greater age also.

Gonad-weight.

The growth of the gonads, like that of any other organ, can be represented by a curve similar to that for the whole animal. In Fig. 1 the curve for gonad-weight is on four times the scale of the body-weight curve. The former is displaced to the right, owing to the initial delay in gonad development, and is at first steeper than the body-growth curve, but after about seven years (five winter-rings) it maintains a fairly constant relation to the body-weight.

The gonad curve is really discontinuous once spawning has occurred for the first time. At this and subsequent spawning times the gonad-weight falls abruptly to zero, whence it re-develops to reach the next datum on the curve in the following season (Fig. 2). These successive maxima fall on a smooth curve which is independent of the total weight of the body.

The gonads are not the only organs which undergo an annual cycle.

Mr. E. Ford has kindly placed at my disposal extensive data on the liver-weight of the mackerel, which passes through a similar cycle, the maxima appearing just before the spawning season. These maxima also lie on an S-shaped curve. Owing to the difficulty of catching herrings of the same class at all seasons of the year, no investigation has been made of the changes which take place in other tissues of the body, except just before and during the spawning season (Bruce, **1**). It appears, however, that even the muscle tissue is depleted to some extent at this time, and that its growth may also be represented by a rhythmic curve with rising

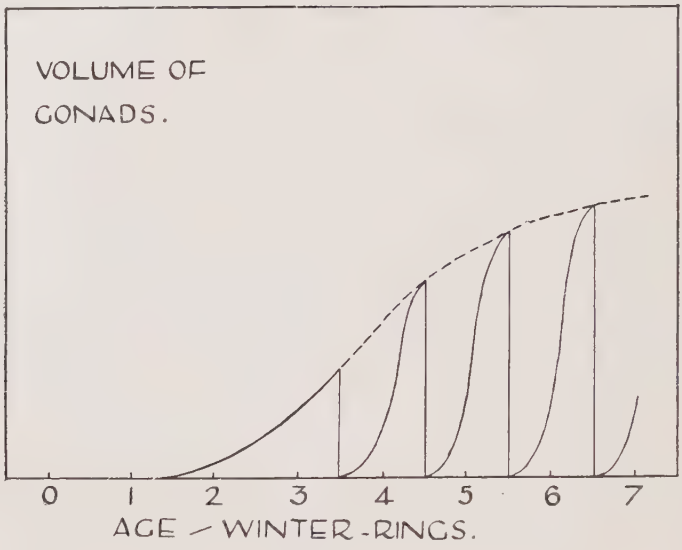

Fig. 2.—Diagram illustrating the discontinuity of gonad development.

maxima. Thus at least two periodic fluctuations are taking place in the body, whose amplitudes are independent. The total body-weight represents the sum of a differential system of organ-growth.

Relation of Gonad-weight to Body-weight.

The data were divided into weight-groups at 10 gm. intervals. The figure given for the weight is the mid-point of the group, and differs slightly from the mean within the group (Tables V and VI). In Figs. 3 and 4 it will be seen that the points, though somewhat scattered, show a high correlation between gonad-weight and total body-weight, and that the line which fits the points most closely is nearly straight. The correlation coefficients which are worked out below, approach sufficiently near to unity to enable a straight line to be used as a working approximation.

The relation which is important here is that of gonad-weight to body-weight. Subsequently it will be necessary to deduce approximate gonad-weights from body-weights, so that the line to be determined is the regression of gonad-weight on body-weight. Gonad-weight is the dependent and body-weight the independent variate. This relation, called the regression function, is given by the formula (Fisher, **2**) :—

$$y=\bar{y}-b(x-\bar{x}),$$

where y is the gonad-weight with mean $\bar{y}$, x is the total body-weight with mean $\bar{x}$; and b is a constant to be determined, called the regression coefficient. It gives the slope of the curve.

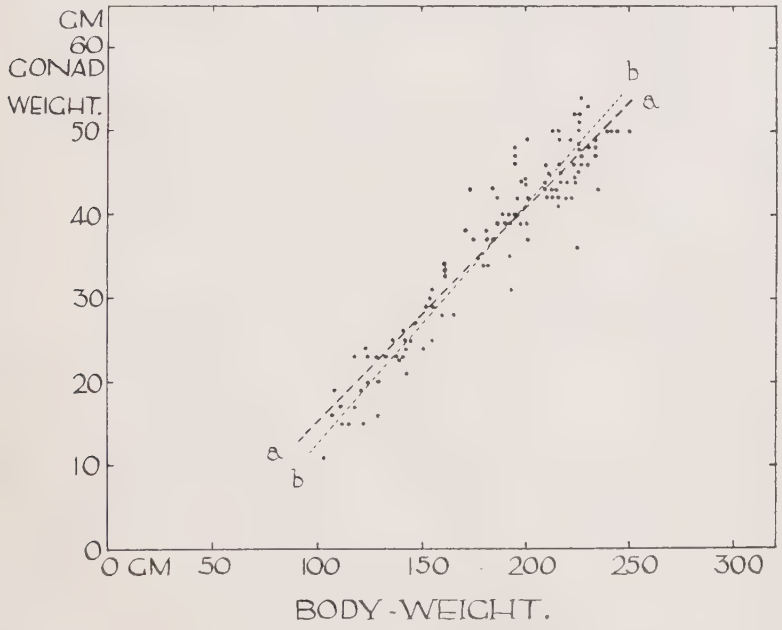

Fig. 3.—Correlation diagram of gonad-weights and body-weights for males of Calf type.

aa. Regression line of gonad-weight on body-weight.
bb. Regression line of body-weight on gonad-weight.

It is important to notice that the regression of body-weight on gonad-weight is not the same as the regression of gonad-weight on body-weight. It would be if the correlation between the two variates were complete (i.e. unity), which it is not. In Figs. 3 and 4 both regression lines are drawn, illustrating the difference. The fact that the regression line evaluated and used below does not appear to fit the points perfectly is liable to deceive unless this distinction is realized.

For the males it is found that

$$\sigma y = \pm 2{\cdot}189 \times 5 \text{ gm.} \qquad \bar{y} = 37{\cdot}26 \text{ gm.}$$
$$\sigma x = \pm 3{\cdot}973 \times 10 \text{ gm.} \qquad \bar{x} = 186{\cdot}5 \text{ gm.}$$

The coefficient of correlation (r) between y and x is 0·949. The regression coefficient (b) is estimated by the formula

$$b = r\frac{\sigma y}{\sigma x} = 0{\cdot}949 \times \frac{2{\cdot}189 \times 5}{3{\cdot}973 \times 10} = 0{\cdot}261$$

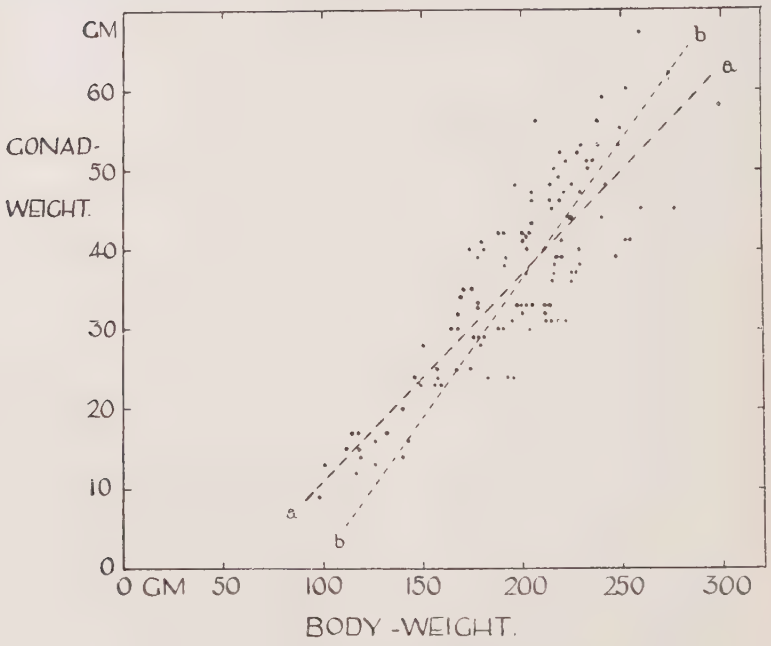

Fig. 4.—Correlation diagram of gonad-weights and body-weights for females of Calf type.

Lettering as in Fig. 3.

Therefore

$$y = 37{\cdot}26 + 0{\cdot}261\,(x - 186{\cdot}5)$$
$$= 0{\cdot}261x - 11{\cdot}5 \text{ gm.}$$

For the females,

$$b = r\frac{\sigma y}{\sigma x} = 0{\cdot}876 \times \frac{(2{\cdot}407 \times 5)}{(3{\cdot}959 \times 10)} = 0{\cdot}266$$

Therefore

$$y = 36{\cdot}33 + 0{\cdot}266\,(x - 197{\cdot}25)$$
$$= 0{\cdot}266x - 16{\cdot}2 \text{ gm.}$$

Though the very close agreement between the regression coefficients of males and females may be fortuitous, there cannot possibly be a significant difference between the two growth-rates. The constants 11·5 and 16·2, which indicate how far the lines are displaced to the right along the x-axis, differ by nearly 5 gm., and it will be necessary to test the significance of this.

Two 25-gm. groups of values were selected where the mean total weights of males and females are the same.

Take x=222·5 gm. (range of weight from 213–237 gm.).

TABLE I.

y gm.	Deviation (d)	Males. Frequency (f)	$f \times d$	$f \times d^2$	Females f	$f \times d$	$f \times d^2$
30	−15	..	..	..	4	−60	900
35	−10	1	−10	100	6	−60	600
40	− 5	6	−30	150	6	−30	150
45	..	16	..	..	8	..	..
50	+ 5	13	+65	325	10	+50	250
55	+10	2	+20	200	2	+20	200
		n=38	+45	775	n=36	−80	2100
Divided by (n−1) since the numbers are small			1·216	20·95		−2·29	60·00
Correction for mean			.(1·216)²	1·48		(−2·29)²	5·23
Correction for grouping			(25×·0833)	2·08			2·08
Corrected estimate of variance				=17·39			=52·69

Standard Error of the means of y_1 (males) and y_2 (females)=s.

$$s^2=\frac{17\cdot39}{38}+\frac{52\cdot69}{36}=0\cdot458+1\cdot463,$$

$$\therefore s=\sqrt{1\cdot921}=\pm1\cdot39 \text{ gm.}$$

Mean y_1=46·22 gm. ; and mean y_2=42·71 gm.

$$\therefore y_1-y_2=3\cdot51 \text{ gm.}$$

Thus in this case the mean difference between testes and ovaries is about 3·5 gm. The points therefore lie closer together than the average (4·7 gm.) ; yet this difference is about 2·5 times its own standard error, so that it may be regarded as definitely significant.

Taking two other pairs of values, where x=199 gm., we find the

difference of the mean gonad-weights to be 6 gm., with a standard error of 1·56 gm. P is therefore rather more than 0·0001, which means that such figures could be explained by coincidence in only one out of ten thousand trials, assuming the samples to be random.

The mean gonad-weights of the whole sample (♂ 37·26, ♀ 36·33 gm.) differ by less than a gram. For this reason it might still be thought that the male and female regression lines of gonad-weight on body-weight are virtually identical. Such confusion arises from the fact that, though the ovaries are lighter than the testes in comparable fishes, the females reach a greater absolute size. The range of ovary weight is thus extended beyond that of testis weight, bringing the mean relatively higher. The total body-weights at which the mean gonad-weights occur (♂ 186·5, ♀ 197·2 gm.) make this clear.

Since the regression functions are used extensively in the following pages, and considerable importance attaches to their reliability, tests have been made to show whether or not the departures from straightness of the lines are significant. These are given in an appendix at the end of the paper. I have to thank Dr. R. A. Fisher for his assistance at this point. His methods have been used throughout this paper, and the sums and calculations are drawn up as nearly as possible on the lines of the examples given in his book (Fisher, **2**). In both sexes of the Calf herring which have been tested, the probability of any departures from linear regression being significant is well below the formal limit (5 per cent.).

Conclusions from Regression Functions.

Certain deductions may be made from this analysis. The males and females have been found statistically distinct in so far that the testes occupy a greater proportion of the total weight than do the ovaries in comparable fishes. The rates of growth of the gonads with respect to body-weight are, however, the same.

The regression lines obtained are approximations to the facts over the range considered. It is not legitimate to produce them to cut the x-axis at 44 and 61 gm., since the real lines are certainly not straight as will be shown below. It is clear, however, that the female gonads lag behind the male at the initiation of development, a lag indicated by 61—44 gm. For if the two sexes were simultaneous in this respect, either the regression lines would be identical, or they would diverge from a common initial point, with different regression coefficients. This is contrary to the observations made previously.

Nor can the observed sexual difference be due to a difference in specific gravities of testicular and ovarian tissue. If this were the case, the coefficients b_1, b_2 could not be the same. The regression lines would

again diverge for increasing values of x, even if they did not have a common origin.*

If the regression equation is applied to the sigmoid gonad curve in Fig. 1, it will be seen how the approximation breaks down if extended beyond the range of observations. By putting successively $y=0$, $x=0$, we should have a curve asymptotic to $-11{\cdot}5$ at the lower end, and reaching the value 0 gm. when $x=44{\cdot}0$ gm. (for the males). This is of course impossible, but it is easily shown that the origin of the curve is near this point, when $x=41$ gm. For instance, if the ratio $\frac{y}{x}$ is calculated, the observed ratios are less than the theoretical values at first, which is to be expected if the origin of the real curve is near this point.

TABLE II.

Age (winter rings)	2	3	4	5	6	7
Observed $\frac{y}{x}\%$	16·46	18·9	19·4	21·2	20·7	21·06
Theoretical $\frac{y}{x}\%$	17·4	18·7	19·9	20·5	20·7	20·9

The gonads thus start to develop in the summer after the first winter ring is laid down, when the males reach a weight of 35 to 50 gm. It is possible that the females have reached a greater size at this time, which would account for the initial difference in gonad-weight, or that the development of their gonads may be delayed somewhat longer. Spawning fishes were not found amongst the Manx herring less than 95 gm. in weight, or having scales with fewer than two winter rings.

"Low" Herrings.

In confirmation of these results, data obtained from samples of the inshore or *Low herring* have been examined in the same way. The data are not so extensive as those for the Calf type, and were collected rather before the height of the spawning season, from July 21st to 29th. They comprise 234 fish, of which 161 were in Stage V, and thus available for comparison with the other samples; 110 were males, and 51 females.

In the same way as before the regressions of gonad-weight on body-weight have been determined. These are not thought to be very reliable,

* The specific gravities of the fresh gonads of six male and six female herrings about to spawn (Stage V) have been determined from Plymouth material. If anything, the testes are lighter than the ovaries. Sp. Gr. of Testes= 1·07(5); Sp. Gr. of Ovaries= 1·08(4).

particularly in the case of the female, but they offer an excellent check upon those found for the other data. The regression functions are :—

for the males, $y=0{\cdot}21(7)x-10{\cdot}45$ gm.,

and for the females, $y=0{\cdot}21(9)x-20{\cdot}3$ gm.

These are also statistically distinct. The coefficients are again almost the same, though the very slight difference observed is certainly due to coincidence. They are considerably smaller than the same coefficients in the Calf samples, due largely to the earlier stage of maturity found in the present case. Stage V is elastic, embracing for 200 gm. fishes a range of male gonad-weight between 30 and 50 gm. ; for this reason there is a notable difference between the earlier and final grades of ripeness found within it.

Age.

The rate of growth of the gonads decreases with advancing age ; and in this sense their increase can be correlated with the number of times the fish has spawned. The more numerous the spawnings, the smaller the annual increase of gonad-weight. Such a correlation would, however, be a false one ; for the growth-rate of the gonads is intimately concerned with that of the whole body, which also becomes smaller with advancing age. There is no other connection with the number of spawning seasons. For, if a number of fish of the same weight are taken, their ages will vary over a small range ; and it is possible to show that among these the older fish, which have spawned more often, have gonads just as large as, and no larger than the younger ones, allowances being made for the variations of different year-classes. A comparison of fishes of roughly the same weights, but of different ages, is the only method of approach to this question.

In the following Table the two 25-gm. weight groups (200 and 225 gm.) have been combined to illustrate this point. The range of weight is from 188 to 237 gm. The mean observed ratio $\frac{y}{x}$ is given, and also the theoretical ratio, calculated from the regression formulæ. The differences between these are slight, and there is no marked increase in the observed values in the older year-groups, such as would be expected if the size of the gonads went on increasing after the general growth had practically ceased.

It may be noticed in addition that the material annually spent in building up the gonad is completely made up before the next season.

For four years after spawning the relative size of the gonad continues to increase (see Table on p. 57) ; there it remains almost constant, and its actual weight increases in linear proportion to the body-weight.

The end of these four preliminary seasons, during which the relative fecundity is rising, is not a turning-point in the death-rate, as far as can be ascertained from the numbers in these and subsequent year-classes.

TABLE III.

Age (winter rings)	3	4	5	6	7	8 & above
MALES						
Frequency	—	7	21	20	9	4
Observed $\frac{y}{x}$%	—	19·8	20·9	20·8	21·2	20·9
Expected $\frac{y}{x}$%	—	20·4	20·7	21·0	20·9	21·1
Difference	—	−0·6	0·2	−0·2	0·3	−0·3
FEMALES						
Frequency	2	8	14	22	12	3
Observed $\frac{y}{x}$%	18·3	17·0	18·9	19·6	18·9	17·7
Expected $\frac{y}{x}$%	18·2	18·2	18·7	19·0	18·9	19·1
Difference	0·1	−1·2	0·2	0·6	0·0	−1·4

TABLE IV.

Age (winter rings)	2	3	4	5	6	7	8 & above
Frequency	80	61	54	83	83	36	37

Both five- and six-ring groups are particularly numerous.

Thus it appears that spawning does not draw on the resources of the fish to a greater extent than can be replaced, with interest, each year. There is no indication of an increasing tax which the fish cannot make up, the effects of which continue to pile up until ultimately they cause its death, in a way that has sometimes been suggested. The growth of the gonads is in harmony with that of the other organs.

There is a notable difference in the absolute sizes of the two sexes. For the Calf type, the mean weight of the females is 197·25 gm., and for the males 186·5 gm. This, however, does not approach the great difference

found in the flat-fishes or the whiting. Owing to the uncertainty of age-determination when the rings become crowded, it is not possible to say whether the females attain a greater age also.

I wish to thank Mr. E. Ford for his constant advice, and Dr. R. A. Fisher, F.R.S., for his kindness in going over the manuscript.

SUMMARY.

From two series of samples of different populations of herrings from the neighbourhood of the Isle of Man, data were obtained of the lengths, weights, gonad-weights, and ages of 396 mature fishes. The growths of the whole body and of the gonads were represented by the upper portions of S-shaped curves. The male and female body-weights are nearly the same at any age over the range considered, but the testes of the male are always heavier than the ovaries of the female in such comparable fishes. The females attain a greater size than the males.

The weight of the gonads bears a linear relationship (as a first approximation) to the total weight of the fish over the range of size considered. The regression functions evaluated for the two sexes are

$$y = 0{\cdot}261x - 11{\cdot}5 \text{ for the males, and}$$
$$y = 0{\cdot}266x - 16{\cdot}2 \text{ for the females,}$$

where y is the gonad-weight and x the total weight of the fish, both in grams. The difference between the weights of testes and ovaries in male and female fishes of the same size is therefore about 4·7 gm., which is shown to be significant. It cannot be due to specific gravity of growth-rate differences, since the regression coefficient (0·26) is the same for both sexes.

It is suggested that the reproductive organs start to develop in the summer following the laying down of the first winter ring on the scales; and that the initial handicap in female gonad-weight may be due to the males being smaller than the females at this time.

Confirmation of the conclusions drawn from the Calf herring is given by a similar analysis of the Low herring samples.

By a comparison of fishes of the same weight but of varying ages, it is shown that the annual loss of tissue at spawning is completely made up during the next twelve months, and that death cannot be due to the increasing tax of spawning ultimately exceeding the animal's powers of recovery.

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2. Fisher, R. A. Statistical Methods for Research Workers. 2nd Ed., Edinburgh, 1928.
3. Pearl, R. Studies in Human Biology. Baltimore, 1924.

TABLE V.

Correlation Table of Gonad-weight and Total Body-weight for Males of the "Calf" Type.

Total Body-weight. (Grams) $= x$.

Gonad-weight (grams) $= y$	105	115	125	135	145	155	165	175	185	195	205	215	225	235	245	255	Total.	Frequency × Deviation.	Frequency × (Deviation)^2.
10	1																1	-5	25
15	1	4	2														7	-28	112
20	1		3		1												5	-15	45
25		1	3	4	6	2											16	-32	64
30						4	2			1							7	-7	7
35							3	1	4	1	1		1				11	0	0
40								1	4	6	2	5	2				20	20	20
45								1	1	3	4	7	8	3			27	54	108
50										1	1	3	7	3	3	1	19	57	171
55													1	1			2	8	32
Total $= n_p$	3	5	8	4	7	6	5	3	9	12	8	15	19	7	3	1	**115**	+52	584
Total excess	-12	-18	-23	-8	-15	-8	-2	+3	+6	+14	+13	+28	+43	+19	+9	+3	+ 52		
Mean excess	4·000	-3·600	-2·875	-2·000	-2·143	-1·333	-0·400	+ 1·000	+0·667	+1·167	+1·625	+1·867	+2·263	+ 2·714	+ 3·000	+3·000	0·4522		
Product	48·00	64·80	66·12	16·00	32·14	10·67	0·80	3·00	4·00	16·33	21·12	52·27	97·31	51·57	27·00	9·00	23·51		
Frequency × Deviation	−24	−35	−48	−20	−28	−18	−10	− 3	0	12	16	45	76	35	18	7	+23		
Frequency × (Deviation)^2	192	245	288	100	112	54	20	3	0	12	32	135	304	175	108	49	1829		
$n_p(x-\bar{x})(y-\bar{y})$	96	126	138	40	60	24	4	−3		14	26	84	172	95	54	21	951		

Note.—All calculations are made in grouping units, i.e. 10 grams for x and 5 grams for y.

TABLE VI.

Correlation Table of Gonad-weight and Total Body-weight for Females of the "Calf" Type.

Total Body-weight. (Grams) $= x$.

Gonad-weight (Grams) $= y$	100	110	120	130	140	150	160	170	180	190	200	210	220	230	240	250	260	270	280	290	300	Frequency Total × Deviation		Frequency × (Deviation)^2
10	1		1																			2	−10	50
15	1	1	4	3	2																	11	−44	176
20					1																	1	−3	9
25						2	4	4	1	1	1											13	−26	52
30						2		3	2	2	3	3	2									17	−17	17
35								2	5		4	3	2	3								19	0	0
40								1	3	4	5		3	3		3						22	22	22
45												2	3	4	1		1		1			12	24	48
50											1	1	4	4	2							12	36	108
55														2	2	2						6	24	96
60															1	1		1			1	4	20	100
65																	1					1	6	36
Total	2	1	5	3	3	4	4	10	11	7	14	9	14	16	6	6	2	1	1	0	1	**120**	+32	714
Total excess	−9	−4	−21	−12	−11	−6	−8	−10	−1	0	+3	+4	+19	+31	+21	+16	+8	+5	+2	0	+5	+32		
Mean excess	−4·500	−4·000	−4·200	−4·000	−3·667	−1·500	−2·000	−1·000	−0·091	0·0	+0·214	+0·444	1·357	1·937	3·500	2·667	4·000	5·000	2·000	0·0	5·000	0·2667		
Product	40·50	16·00	88·20	48·00	40·33	9·00	16·00	10·00	0·09	0·0	0·64	1·78	25·78	60·05	73·50	42·67	32·00	25·00	4·00	0·0	25·00	8·533		
Frequency × Deviation	−20	−9	−40	−21	−18	−20	−16	−30	−22	−7	0	+9	28	48	24	30	12	7	8	0	10	−27		
Frequency × (Deviation)^2	200	81	320	147	108	100	64	90	44	7	0	9	56	144	96	150	72	49	64	0	100	1901		
$np(x-\bar{x})(y-\bar{y})$	90	36	168	84	66	30	32	30	2	0	0	4	38	93	84	80	48	35	16	0	50	986		

Note.—All calculations are made in grouping units, i.e. 10 grams for x and 5 grams for y.

APPENDIX.

These tests of the straightness of the regression lines follow the method given by Fisher (**2**, pp. 216–223). The steps of the calculation are arranged consecutively, and are intended to be read in conjunction with Dr. Fisher's book, where a similar case is described in full. Tables 50 and 51 in his example correspond to Table V for the males and Table VI for the females in mine.

(*a*) *Males.*

TABLE VII

	Estimate.	Correction for Mean.	Corrected Estimate.
$\Sigma(y-\bar{y})^2$	584	$-\frac{52^2}{115}$	560·5
$\Sigma(x-\bar{x})^2$	1829	$-\frac{23^2}{115}$	1824·4
$\Sigma(x-\bar{x})(y-\bar{y})$	951	$-\frac{52\times 23}{115}$	940·6

From Table V,

Sum of Products in first 16 arrays = 520·14
Product in final array = 23·51

$\Sigma[n_p(\bar{y}_p - \bar{y})^2]$ = 496·63

From Table VII, $\Sigma(y-\bar{y})^2$ = 560·5

TABLE VIII.

Variance.	Degrees of Freedom.	Sum of Squares.	Mean Square.
Between Arrays	15	496·6	..
Within Arrays	99	63·9	0·645
Total	114	560·5	

$$\Sigma(x-\bar{x})^2 = 1842{\cdot}4$$
$$\Sigma(x-\bar{x})(y-\bar{y}) = 940{\cdot}6$$
$$\therefore \frac{[\Sigma(x-\bar{x})(y-\bar{y})^2]}{\Sigma(x-\bar{x})^2} = \frac{(940{\cdot}6)^2}{1824{\cdot}4} = 485{\cdot}0.$$

TABLE IX.

Variance between Arrays due to :—	Degrees of Freedom.	Sum of Squares.	Mean. Square.
Linear regression	1	485·0	..
Deviations from regression	14	11·6	0·83
Total	15	496·6	

TABLE X.

Mean Square.	Natural Log.	½ Log.
0·83	−0·1863	−0·093
0·645	−0·4385	−0·219
	Difference (z)	=0·126

Thus z is 0·126, and since the 5 per cent point is about 0·29 (**2**, p. 212), there is absolutely no significant departure from linear regression.

(*b*) *Females.*

TABLE XI.

	Estimate.	Correction for Mean.	Corrected Estimate.
$\Sigma(y-\bar{y})^2$	714	$-\frac{32^2}{120}$	705·5
$\Sigma(x-\bar{x})^2$	1901	$-\frac{(-27^2)}{120}$	1894·9
$\Sigma(x-\bar{x})(y-\bar{y})$	986	$+\frac{32\times 27}{120}$	993·2

From Table VI,

Sum of Product in first 21 arrays =558·54
Products in final array = 8·53
$\Sigma[n_p(\bar{y}_p-\bar{y})^2]$ =550·01
From Table XI, $\Sigma(y-\bar{y})^2$ =705·5

TABLE XII.

Variance.	Degrees of Freedom.	Sum of Squares.	Mean Square.
Between Arrays	20	550·0	..
Within Arrays	99	155·5	1·571
Total	119	705·5	

$$\Sigma(x-x)^2 = 1894{\cdot}9$$
$$\Sigma(x-\bar{x})(y-\bar{y}) = 993{\cdot}2$$
$$\therefore \frac{[\Sigma(x-\bar{x})(y-\bar{y})]^2}{\Sigma(x-\bar{x})^2} = \frac{(993{\cdot}2)^2}{1894{\cdot}9} = 520{\cdot}6.$$

TABLE XIII.

Variance between Arrays due to :—	Degrees of Freedom.	Sum of Squares.	Mean Square.
Linear regression	1	520·6	..
Deviations from regression	19	29·4	1·547
Total	20	550·0	

TABLE XIV.

Mean Square.	Natural Log.	½ Log.
1·547	0·436	0·218
1·571	0·452	0·226
	Difference (z)	$=-0·008$

The probability that any departures from the female regression line are significant is therefore infinitesimal.

Note on a Sailfish (*Istiophorus americanus* Cuvier and Valenciennes) new to the British Fauna.

By

J. R. Norman.

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With 2 Figures in the Text.

About 9 a.m. (flood tide) on 17th August, 1928, a large sailfish was captured in a dying condition in the main channel of the Yealm estuary, South Devon, opposite the Yealm Hotel, about a mile above the Yealm Bar. The fish was carefully packed up by Mr. V. C. Wynne-Edwards, and promptly despatched to the British Museum (Natural History), where the plaster cast shown in the accompanying illustration (Fig. 1) was prepared by Mr. S. Stammwitz. The specimen was then cut into two pieces and preserved in alcohol.

Owing to the difficulty of preserving these large fishes in museums, except as stuffed skins, and to the marked changes which they appear to exhibit at different stages of growth, our knowledge of the group which includes the swordfishes, sailfishes, and spearfishes is decidedly limited, and the identification of species is a matter of some difficulty.*

In a recent monograph,† Jordan and Evermann distinguish nine species of *Istiophorus*, of which five are said to be new to science. The descriptions of four of these new species are based solely on photographs, the fifth being described from a plaster cast in the museum at Honolulu. As suggested by the authors themselves, some of the characters used by them in their key to the species may be "matters of age not indicating specific distinction." According to this key, the present specimen from Devonshire would appear to be referable to one of their new species—*I. maguirei* from the West Indies, but, so far as I am able to judge from the description and photograph, there seems to be no valid reason for separating this from *I. americanus*, which is found on the Atlantic coast of America from Brazil northwards to Cape Cod and beyond.

The first mention of the species in question, indeed, the first allusion to a sailfish, is to be found in Piso's *Historiæ Rerum Naturalium Brasiliæ*

* For a complete summary of our knowledge of the group up to that date, see Goode, Rep. U.S. Fish. Comm. (1880), 1883, pp. 289–386, pls. I–XXIV.

† Occ. Papers Calif. Acad. Sci., XII, 1926, 113 pp., 20 pls.

. . . printed at Amsterdam in 1648. In this work a few lines of description and a crude but recognisable figure are given by Marcgrave (p. 171), who gives the fish the name of "*Guebucu brasiliensibus.*" No species of this genus was systematically described until 1786, when Broussonet* published a description based on a specimen and a drawing made by Sir Joseph Banks, giving the fish the name of *Scomber gladius*. The type of this species, a stuffed skin eight feet in length, is preserved in the collection of the British Museum, and was said to have come from "La Mer des Indes." In 1802, Lacepède† established the genus *Istiophorus* for this species. In 1831, Cuvier and Valenciennes‡ founded the species *I. americanus* on the figure in Piso and Marcgrave's work, and redescribed the Indian species as *I. indicus*, ignoring for some unknown reason Broussonet's earlier name. According to Cuvier and Valenciennes, *I. americanus* occurs also on the Atlantic coast of Africa, and they mention a specimen seven feet in length figured by Barbot, which had been caught off Commendo. This is the only reference I have been able to trace of the species occurring on the eastern side of the Atlantic, unless the young specimen caught between France and the Cape of Good Hope, and described by Cuvier and Valenciennes§ as *Histiophorus pulchellus*, should prove to be identical with *I. americanus*.

Several authors have expressed doubt as to whether *I. americanus* is specifically distinct from *I. gladius*, and the two species were united by Günther and Lütken. No attempt has been made previously to compare specimens of similar size, and I take this opportunity of publishing a description of the specimen from Devonshire, and also of Broussonet's type specimen of *I. gladius*, which I regard as representing a distinct species.

Istiophorus americanus, Cuv. & Val. (Figs. 1, 2).

Depth of body about $6\frac{1}{2}$ in the length (from tip of sword to base of caudal), length of head nearly 3. Distance from tip of sword to anterior margin of eye about twice the length of rest of head; diameter of eye $3\frac{1}{2}$ in postorbital part of head, interorbital width $1\frac{3}{5}$. Sword narrow, regularly tapering, nearly twice as broad as deep, its upper and lower surfaces both rounded. Maxillary extending to a little beyond eye: jaws with bands of minute, conical teeth, which extend forward on to the lateral and ventro-lateral surfaces of the sword. Dorsal XXXV (+VIII), 7; the whole fin depressible into a deep groove which extends nearly to the origin of the soft dorsal; origin of spinous dorsal above operculum; outline of fin irregular, the longest spines about middle of fin, $1\frac{1}{3}$ in length of head; last visible spine followed by eight short, stiff, stub-like spines,

* Mem. Acad. Sci., 1786, p. 454, pl. 10.
† Hist. Nat. Poiss., III, p. 374.
‡ Hist. Nat. Poiss., VIII, p. 293.
§ *l.c.*, p. 305.

FIG. 1.—Plaster cast of specimen of Sailfish (*Istiophorus americanus*) from the Yealm Estuary, South Devon.

FIG. 2.—Ventral view of the fresh specimen, showing the groove for the reception of the pelvic fins.

which are completely hidden in the groove, and decrease in size posteriorly; soft dorsal separated from the last stub-like spine by a distance which is a little greater than diameter of eye. Anal 9+7; origin of first anal fin, which is depressible into a groove, below 33rd dorsal spine; origin of second anal about level with that of soft dorsal. Pectoral a little less than $\frac{1}{2}$ length of head. Pelvic slender, tapering, about $1\frac{2}{5}$ in length of head, depressible into a deep groove which extends backwards nearly to the vent (Fig. 2). Upper lobe of caudal $1\frac{3}{5}$ in length of head. Caudal peduncle with two strong, parallel keels on either side. Brownish above, silvery grey below; all the fins greyish brown, the spinous dorsal with a number of small, round, dark spots on the membrane between the spines.

The principal dimensions of the specimens are as follows:—

Total length	2260 mm.
Length to base of caudal	1882 mm.
Greatest depth of body	290 mm.
Total length of head	647 mm.
Length from tip of sword to anterior margin of eye	429 mm.
Diameter of eye	47 mm.
Interorbital width	100 mm.
Length of first dorsal spine	315 mm.
Length of longest dorsal spine	485 mm.
Length of pectoral	305 mm.
Length of pelvic	450 mm.

Istiophorus gladius (Broussonet).

Depth of body 6 or 7 times in the length, length of head nearly 3. Distance from tip of sword to anterior margin of eye nearly $2\frac{1}{2}$ times the length of rest of head; diameter of eye $3\frac{1}{2}$ in postorbital part of head, interorbital width $1\frac{2}{3}$. Sword and teeth similar to those of *I. americanus*. Dorsal XLV, 7; origin of spinous dorsal above operculum; outline of fin apparently irregular, the longest spines about middle of fin, longer than head; all the spines are visible, and decrease gradually in length posteriorly;* origin of soft dorsal separated from last spine by a distance which is little greater than diameter of eye. Anal 14 (or 13)+7; origin of first anal fin below 35th dorsal spine; origin of second anal about level with that of soft dorsal. Pectoral about $\frac{1}{2}$ length of head. Pelvic slender, tapering, $1\frac{1}{4}$ in length of head. Upper lobe of caudal nearly $1\frac{1}{2}$ in length of head. Caudal peduncle with two strong, parallel keels on either side.

* The depth of the grooves for the reception of the fins, and the extent to which the posterior dorsal spines are hidden, is not apparent in this stuffed skin.

The principal dimensions of the specimen are as follows :—

Total length	2458 mm.
Length to base of caudal	2058 mm.
Greatest depth of body	270 mm.
Total length of head	705 mm.
Length from tip of sword to anterior margin of eye	500 mm.
Diameter of eye	50 mm.
Interorbital width	90 mm.
Length of first dorsal spine	345 mm.
Length of highest dorsal spine	820 mm.
Length of pectoral	356 mm.
Length of pelvic	520 mm.

This species differs from *I. americanus* chiefly in the longer sword, larger spinous dorsal fin, with higher posterior rays, longer anal fin, and in the longer pelvics.

Galatheascus striatus—a New Rhizocephalan.

By

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With 6 Figures in the Text.

A specimen of *Galathea strigosa* (L.) with a parasite of fairly large size at the abdomen was collected at the Looe–Eddystone Grounds near Plymouth on June 11th, 1913. Since then the decapod with its parasite has been in the collection of the Laboratory of the Marine Biological

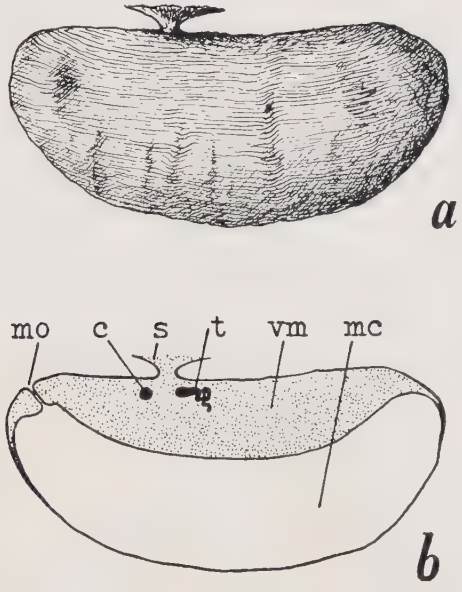

Fig. 1.—*Galatheascus striatus*. *a*, the animal from the left side; *b*, semidiagrammatic longitudinal section in which the genital organs of one side are shown also; *mo*, mantle opening; *c*, colleteric gland; *s*, stalk; *t*, testis; *vm*, visceral mass; *mc*, mantle cavity. ×3.

Association. The specimen is different from all other parasites known to infest the species of the genus Galathea: at a first superficial inspection no mantle opening could be detected, and consequently it remained

doubtful whether the parasite belonged to the Rhizocephala or to some other group of Crustaceans. At my request Dr. E. J. Allen kindly put the animal at my disposal for further investigation. Fortunately the mantle cavity contained an enormous mass of nauplius larvæ, which proved that the parasite belongs to the Rhizocephala, as these larvæ have well-developed frontal horns (Fig. 6).

After some fragments of the mantle had been cut off for the study of its chitinous coverings a series of transverse sections was made from

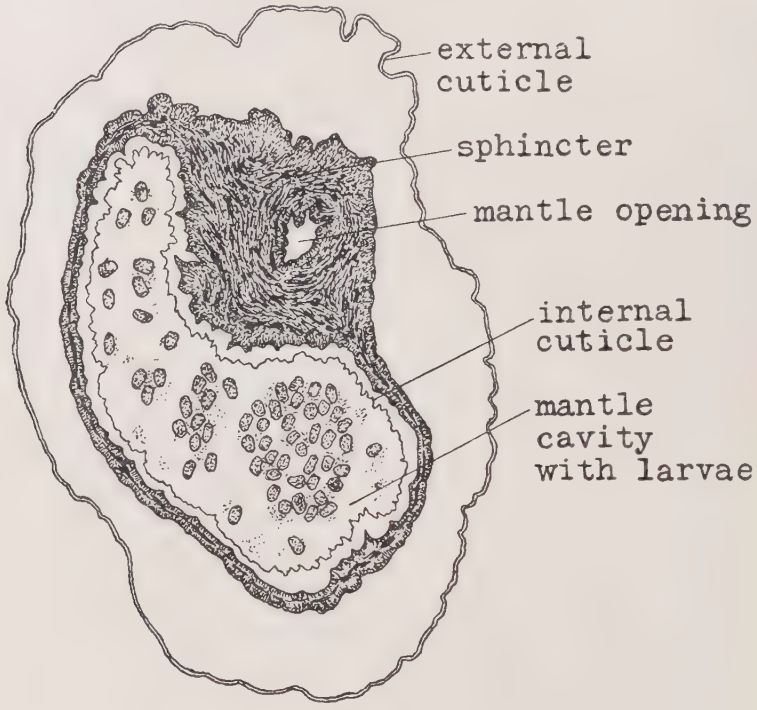

Fig. 2.—Transverse section through the anterior part of the body of *Galatheascus striatus*. The chitinous sheaths of both surfaces of the mantle have loosened from the muscular part. ×18.

the whole animal. The study of its internal anatomy shows that the specimen is closely allied to Peltogaster and consequently has to be classified in the family Peltogastridæ. There are, however, sufficient characteristics which distinguish the specimen from the species of the genus Peltogaster to establish a separate genus, which may be called *Galatheascus*. The diagnosis of this genus is as follows :—

Galatheascus n. g. Body elongate oviform, mesentery very broad, extending from the anterior to the posterior extremity. Stalk in the anterior half of the body. Mantle opening extremely narrow. Colleteric

glands small, simple, in the neighbourhood of the stalk. Testes consisting of a very small straight part at each side of the median plane and a strongly coiled portion which passes into the vasa deferentia ; the whole of the male genital organs in the region of the stalk.

The type species of this genus may be characterised especially by

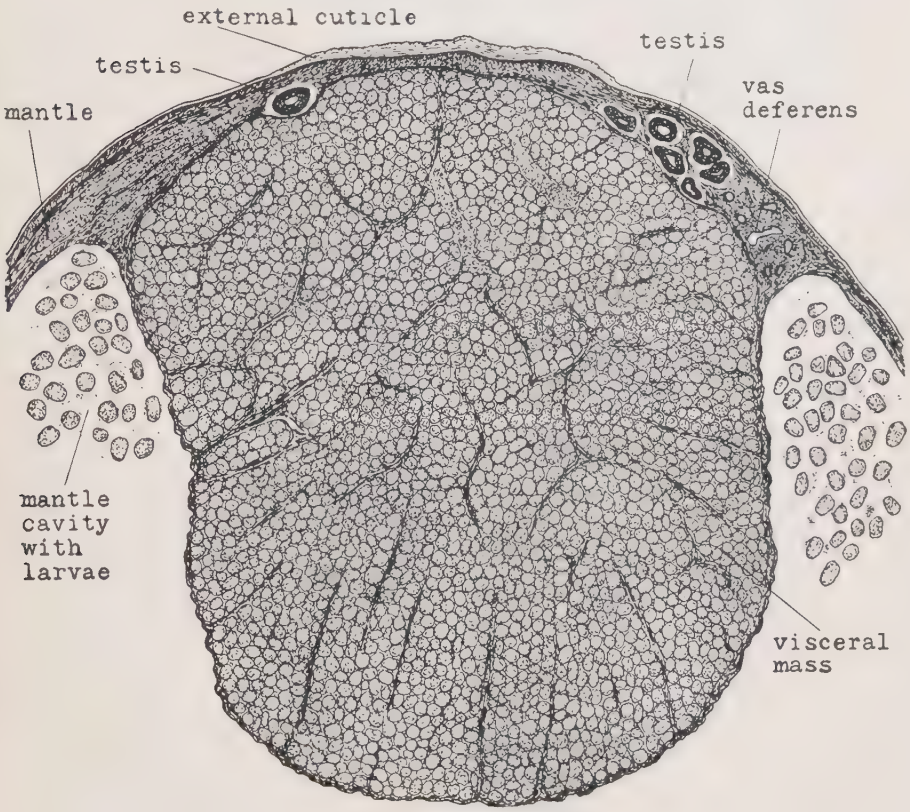

Fig. 3.—Transverse section through the region of the stalk of *Galatheascus striatus*. ×20.

the structure of the chitinous parts of the mantle. So the following diagnosis of the species can be given :—

Galatheascus striatus n. sp. External cuticle of the mantle smooth, with shallow grooves extending over the surface in longitudinal direction. These grooves are about 0·2 mm. apart. The internal cuticle bears retinacula containing one to three spindles each. These spindles have a length of 20 to 25 μ.

A more elaborate description of the peculiarities of the only available specimen is given below.

The parasite was attached to the ventral surface of a specimen of *Galathea strigosa* (L.), between the second and the third abdominal segment. Its longitudinal axis had a direction perpendicular to that of its host ; the anterior pole of the parasite was directed toward the right side of the host. The mantle opening is so small (diameter less than 0·5 mm.) that it escaped notice until the parasite could be studied in the series of sections. One of the most striking differences from the species of the genus Peltogaster is caused by the position of the stalk, which in Galatheascus is found in the anterior half of the dorsal surface (Fig. 1 *a*, *b*), whilst in Peltogaster the stalk is inserted to the mantle in the posterior

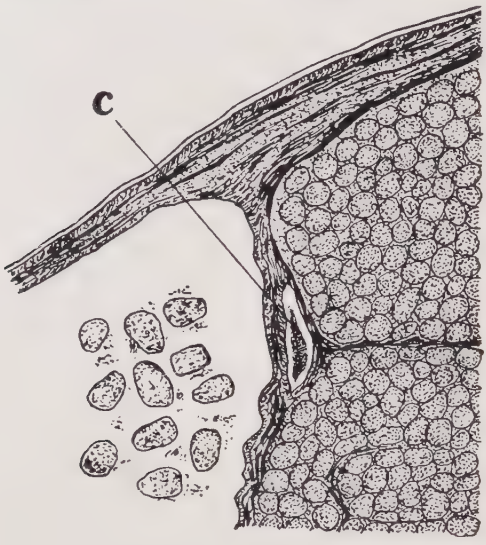

Fig. 4.—Part of a transverse section through *Galatheascus striatus*, slightly nearer to the anterior pole than that of Fig. 3, showing the colleteric gland (*c*). ×36.

part of the body. In Galatheascus the stalk itself is slender, about 1 mm. thick, and very short. It is surrounded by an inconspicuous shield-like thickened part of the external cuticle ; in Fig. 3 this thicker part of the chitin is visible. Muscles are present especially in the dorsal part of the animal and in the mantle. Moreover, the small mantle opening and the narrow tube connecting this opening with the mantle cavity are surrounded by an extremely strongly developed sphincter (Fig. 2). Besides these there is a thin layer of muscles enveloping the visceral mass. Between the groups of eggs in the ovary, which occupies almost the whole of the visceral mass, there are sparsely distributed muscular elements (cf. Fig. 3).

In the neighbourhood of the stalk the genital organs are found

(cf. Fig. 1 *b*). The structure of the testes does not differ in any significant detail from those of Peltogaster; the course of these organs, however, is different. Their closed extremity is directed toward the anterior pole; along a short distance they are straight, but soon the tubes continue their course in a very irregular coiled manner. As a result in sections through this region the lumen of the testis appears several times. One of the testes lies slightly behind the other, consequently in Fig. 3 the posterior part of one and the anterior part of the other testis is visible. After the coiled part of the testis this organ passes into the vas deferens, which has a much thinner wall and is less conspicuous; this part of the

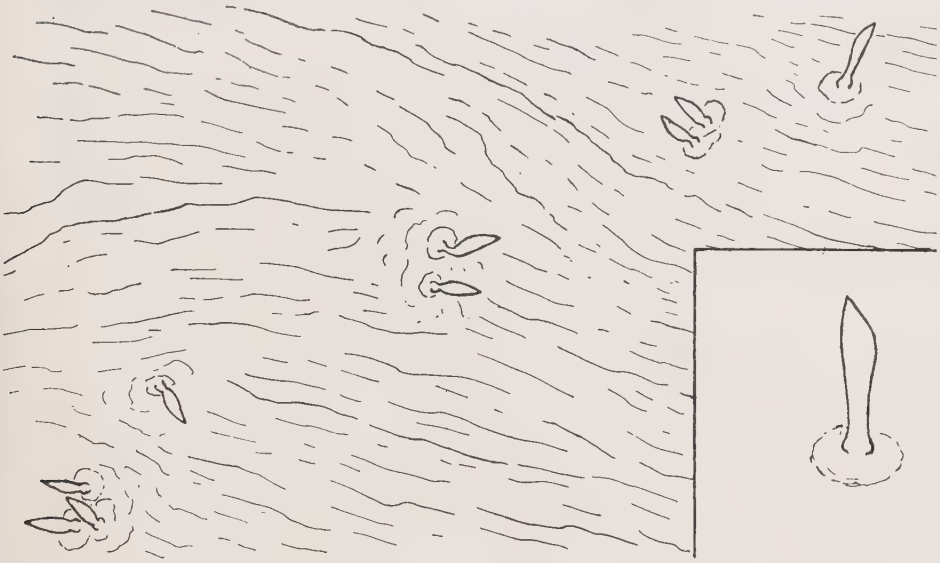

Fig. 5.—Retinacula on the internal cuticle of *Galatheascus striatus*. ×380. In the right-hand corner of the figure one retinaculum more strongly enlarged (×880).

male genital organs also has a strongly irregular course. It terminates with the male genital opening which opens into the mantle cavity.

The colleteric glands have a very minute size: their diameter is less than 0·5 mm. They have an approximately circular lumen which is flattened in a lateral direction. On each side of the visceral mass, close to the insertion of the mantle, one of these organs is found. Inside the glands contain a coagulated mass, obviously the product of secretion of the gland cells. In general the colleteric glands of Galatheascus are built on the same plan as those of Peltogaster; they are probably even more simple than those of the latter genus.

With the exception of the shield-like part round the stalk the external cuticle of the mantle is comparatively thin (8–11 μ). In many parts of the

mantle it has loosened from the muscular elements (e.g. in the anterior part; cf. Fig. 2). The same holds true for the internal cuticle. The surface of the external cuticle is smooth except for the shallow longitudinal grooves mentioned above.

The internal cuticle of the mantle possesses a great number of retinacula (Fig. 5). Many of these consists of a single spindle, others have two, and others again three. The spindles are slender, pointed at the top, and do not bear barbs. In general they are like those of *Peltogaster paguri*, though they are of somewhat larger size (in *P. paguri* about 16 μ, in Galatheascus 20–25 μ).

The larvæ (Fig. 6) are strongly reminiscent of those of Peltogaster

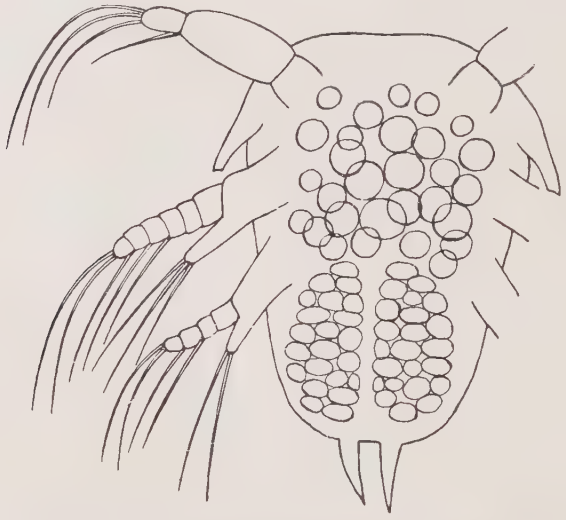

Fig. 6.—Nauplius larva of *Galatheascus striatus*, ventral view. ×250.

(cf. Nilsson-Cantell, 1921); they also have approximately the same size, the total length on an average amounting to 250 μ. In the nauplius of Galatheascus the lateral horns are directed more strongly backwards than in those of Peltogaster. For more particulars on the shape of the legs, etc., I refer to the figure. Probably on account of the insufficient state of preservation, the mouth parts and the frontal filaments could not be found. The eye also is invisible, so in all probability in the living larvæ it was devoid of pigment.

Galatheascus striatus is the first Peltogastrid known to infest a host belonging to the Galatheidæ. Other Rhizocephalid parasites are known to occur on Galatheidæ, but these are representatives of the genus Lernæodiscus (family Lernæodiscidæ, cf. Boschma, 1928). The only

Rhizocephalid hitherto known as a parasite of *Galathea strigosa* is the form designated by Smith (1906) as the new species *Lernæodiscus strigosæ*, the diagnosis of which, however, is very incomplete. According to Smith it differs from *Lernæodiscus galatheæ* by having a very wide " anterior " hinge of the mesentery.

The position of *Galatheascus striatus* to its host differs from that in the other Peltogastridæ : the long axis of Galatheascus is perpendicular to that of its host. Consequently the diagnosis of the family Peltogastridæ as given in a previous paper (Boschma, 1928) has to be amended, the statement " long axis parallel to long axis of host " cannot remain in this diagnosis.

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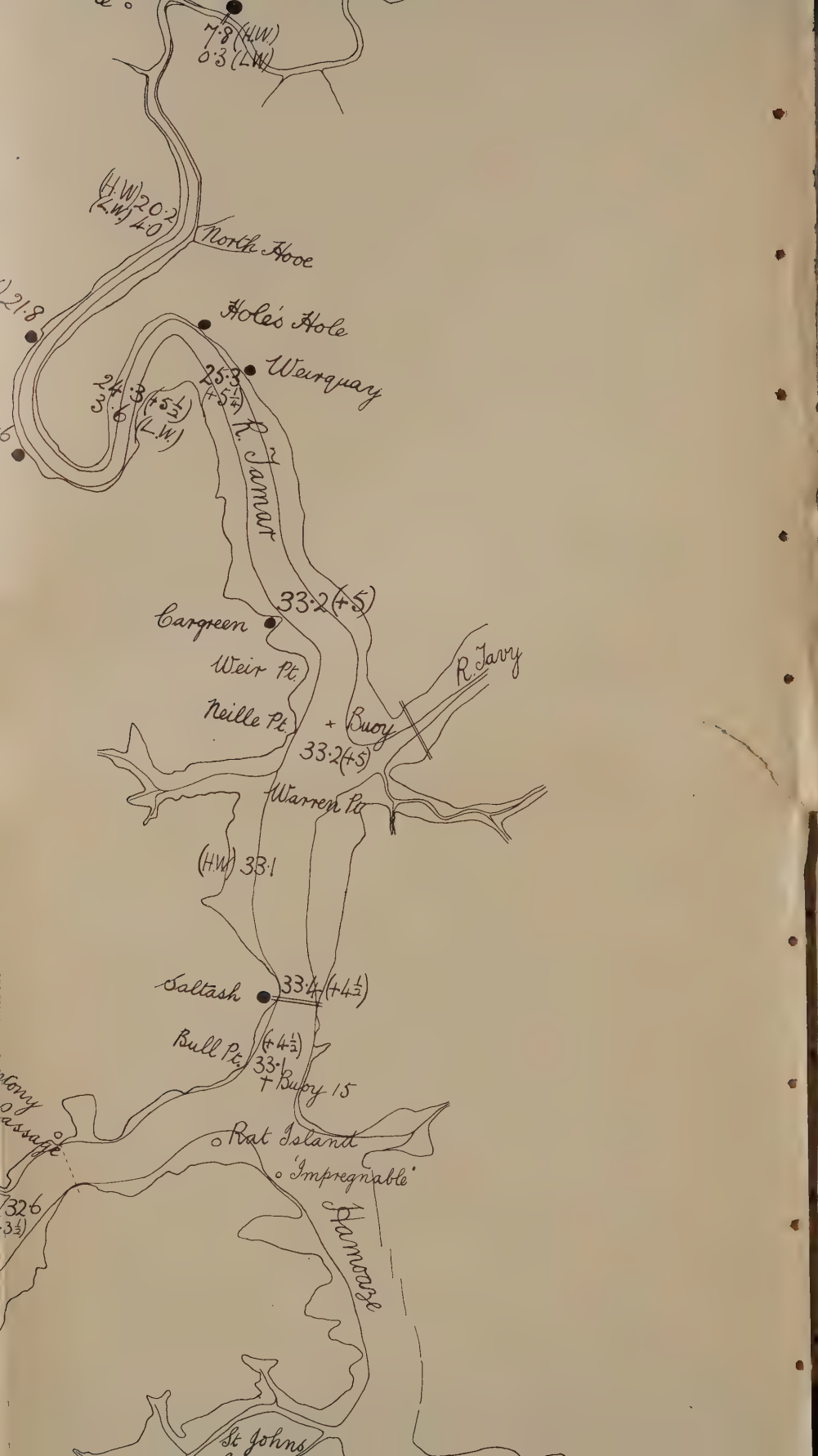
7·8 (H.W.)
0·3 (L.W.)
(H.W.) 20·2
(L.W.) 4·0
North Hooe
Holes Hole
Weirquay
24·8 (+5½)
3·6 (L.W.)
25·3 (+5½)
R. Tamar
33·2 (+5)
Cargreen
Weir Pt.
Neille Pt.
+ Buoy
33·2 (+5)
R. Tavy
Warren Pt.
(H.W.) 33·1
Saltash
33·4 (+4½)
Bull Pt.
(+4½)
33·1
+ Buoy 15
Rat Island
'Impregnable'
Hamoaze
St Johns

A Report on the Fauna of the Estuaries of the River Tamar and the River Lynher.

By

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With 1 Figure in the Text and 1 Chart.

The following is an account of a faunistic investigation covering those parts of the Rivers Tamar and Lynher which are affected by the tide, and was carried out during a period of six months from June to November, 1928.

Description of the Area.

The Tamar forms a portion of the boundary between Devon and Cornwall and flows in a southerly direction along a more or less winding course. (Chart.) The extent of the stream dealt with is from Plymouth Sound to Weir Head, some 19 miles inland measured along the water-course. For about 6 miles downstream from Weir Head, the valley is rather narrow with rock exposures at different places on the convex side of bends, the water being confined to a well-defined channel with steep sides, which are uncovered by the vertical contraction of the stream at low water. The remainder of the river, down to the sea has, generally, a mud-bank on each side, except at occasional bends where rock is present, which is exposed at low water by the lateral contraction due to reduction in level. The upper 4 miles of this region has narrower mud-banks than has the lower portion. These mud-banks or -flats are for the greater part more or less plane surfaces, which may slope gradually into the bed of the main channel, as happens in the lower portion of the area, or they may slope suddenly downwards at the edge, thus forming a well-marked bank to the main channel. In many cases their landward edges lie below high-water neap tide, but in others they slope imperceptibly into the adjoining land surface. In the former cases there is often a low cliff of about 2 feet bordering salt-marsh.

The constitution of the deposit has not been examined, but superficial observation shows that it is generally greyish to black mud of varying consistency, from tough clay-like material into which a man of 168 lbs. may sink to a depth of about 6 inches, to thin "slurry" into which he

may sink to a depth of about 3 feet. The greater part of the area examined has mud into which he may sink to a depth of from 9 inches to 18 inches. The thinner mud is generally greyish, and the tougher usually black. St. John's Lake and a flat above Saltash Bridge on the left bank have a flora of Zostera, growing on a mud of medium consistency in which walking is difficult.

The banks in the upper 4 miles of the mud-flat region, where there is an abrupt slope into the main channel, are of interest on account of a change in character of the deposit along the sharp slope. The fine mud extends downwards roughly half-way, to about half-tide mark, and below there is a change to a coarse-grained material, in some cases having grains of about 1·5 mm. diameter. Such a substratum is quite hard and clearly sandy. The reason for this is largely to be sought in the effect of the rising tide, which passes along the channel with considerable force and lifts the deposit up. The fine material is carried along upstream, and, as further rising goes on, the stream, at about half-tide, commences to spread laterally over the banks, so that a reduction in forward movement is effected with a corresponding fall in the transporting power of the current. Thus suspended material is precipitated in graded series, the fine material being laid on the broad mud-flat and the coarse on the lower part of the slope. The spreading of the water over the upper surface of a mud-flat is a gentle process, and although there is erosion it is only relatively slight, apparently a very thin layer being involved. Some time before high-water most of the lifted material is redeposited, and the turbid stream at the beginning of the tidal flow ultimately becomes relatively clear.

In the lower 9 miles or so, where the mud-flats slope gently into the main channel, this strong scouring does not appear to take place, and the water spreads gently over the banks with disturbance of little more than the merest superficial layer.

On the convex side of bends with rocky ground there is usually a thin layer of mud, which is lifted at the flow and deposited at slackening of the tide. These places are usually not densely populated, since conditions are changing too violently. If *Fucus vesiculosus* is present there is always a fauna, but if it is absent then the fauna is scanty.

Rocky shores are found at places in the upper 6 miles, at the large double bend above Hole's Hole to Pentillie, at Neille Point, and along the shores of the Hamoaze, below Saltash. Alongside the rock in several places the depth of water may be 20 feet to 30 feet. From the Saltash region downwards the depth is considerably more.

The portion of the River Lynher, or St. Germans River,* which is

* The Lynher, which is the longer, flows into the St. Germans River about half a mile east of St. Germans.

dealt with, consists of a length of about 8 miles extending downwards in a roughly south-easterly direction for about 4 miles, and then approximately north-easterly for the same distance, when it joins the Tamar about $3\frac{3}{4}$ miles from the Sound. It also shows two quite well-marked regions, the lower one being about $6\frac{1}{2}$ miles long and the upper (St. Germans), having the characters of the upper 6 miles of the Tamar, extending about $1\frac{1}{2}$ miles, as far as Tideford. The lower $6\frac{1}{2}$ miles have mud-banks corresponding in character with those of the Tamar, i.e. with sharply sloping margins forming the banks of the channel, or with gently sloping surfaces, which gradually pass into the main channel.

The lower 4 miles present a fairly uniform appearance, the fall being slight, but the upper has very rapid transitional stages from the fresh-water region to the brackish area, as the fall is much more marked, the whole tidal length of the St. Germans being 8 miles from Bull Point to Tideford, as compared with about 16 miles from Bull Point to Weir Head. Judging from the fauna, the 4 miles or so from Sheviock Wood to Tideford corresponds with the length of the Tamar upwards from half a mile below Pentillie Quay, a distance of about 9 miles. The same general agreement is seen in the physical nature of the two regions.

Where there are well-marked bends there are usually deposits of plant detritus on the concave side of the bend. These are known locally as " Point-stuff," and serve as sources of manure. They also play a part in the nutrition of many animals, which live on and about them. Beds of " Point-stuff " occur more commonly in the Tamar above Hole's Hole. In the river above St. Germans, the bends are short and, although plant detritus is found, it is not nearly so extensive as in the other river.

Observations on the Salinity* of the Water.

Water samples were taken at various times and places. Owing to the circumstances which governed the work it was not possible to sample the two rivers on the same day. The tidal flow is rapid, high water at Calstock, 13 miles up, being about 23 minutes later than at Plymouth. The result of this was that samples taken at different places on the same day were not comparable, since the state of the tide was different at any two places visited. An attempt was made to obtain approximately comparable results by visiting stations at, as nearly as possible, the same state of the tide. During the present summer, when sampling was carried out, the rainfall was negligible, 3·38 inches being registered at Plymouth during 86 days, so that any disturbance due to excessive fresh water was eliminated. The chief disturbing factor was the variation in the size of the tide, not only from spring tide to neap tide, but in the

* Total weight of salts in grammes per 1000 gms. of sea-water.

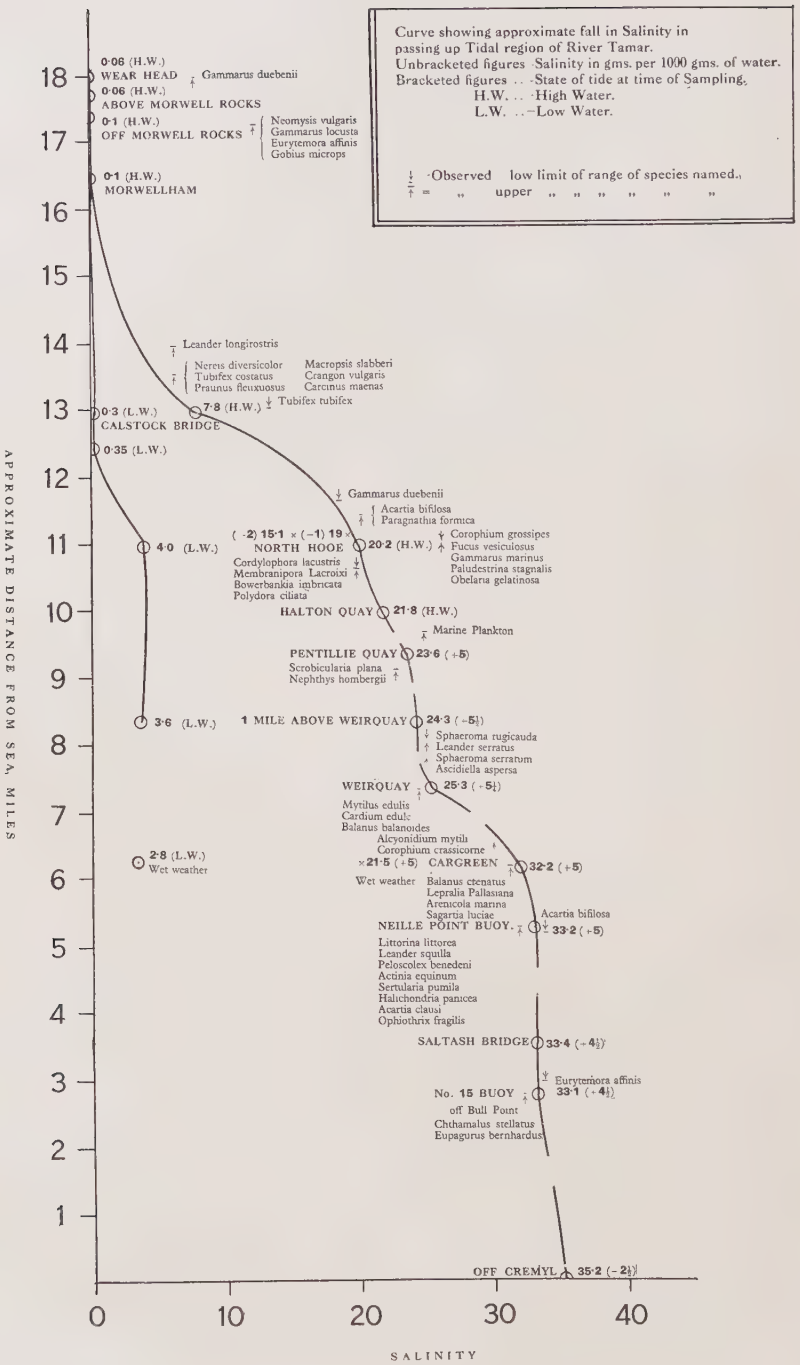
Curve showing approximate fall in Salinity in passing up Tidal region of River Tamar.
Unbracketed figures ·Salinity in gms. per 1000 gms. of water.
Bracketed figures ··State of tide at time of Sampling.
H.W. ··High Water.
L.W. ··Low Water.
Observed low limit of range of species named.
upper
0·06 (H.W.) WEAR HEAD
Gammarus duebenii
0·06 (H.W.) ABOVE MORWELL ROCKS
0·1 (H.W.) OFF MORWELL ROCKS
Neomysis vulgaris
Gammarus locusta
Eurytemora affinis
Gobius microps
0·1 (H.W.) MORWELLHAM
Leander longirostris
Nereis diversicolor
Tubifex costatus
Praunus flexuosus
Macropsis slabberi
Crangon vulgaris
Carcinus maenas
7·8 (H.W.) Tubifex tubifex
0·3 (L.W.) CALSTOCK BRIDGE
0·35 (L.W.)
Gammarus duebenii
Acartia bifilosa
Paragnathia formica
4·0 (L.W.)
(-2) 15·1 × (-1) 19 ×
NORTH HOOE 20·2 (H.W.)
Corophium grossipes
Fucus vesiculosus
Gammarus marinus
Paludestrina stagnalis
Obelaria gelatinosa
Cordylophora lacustris
Membranipora Lacroixi
Bowerbankia imbricata
Polydora ciliata
HALTON QUAY 21·8 (H.W.)
Marine Plankton
PENTILLIE QUAY 23·6 (+5)
Scrobicularia plana
Nephthys hombergii
3·6 (L.W.)
1 MILE ABOVE WEIRQUAY 24·3 (+5½)
Sphaeroma rugicauda
Leander serratus
Sphaeroma serratum
Ascidiella aspersa
WEIRQUAY 25·3 (+5½)
Myrilus edulis
Cardium edule
Balanus balanoides
Alcyonidium mytili
Corophium crassicorne
2·8 (L.W.) Wet weather
×21·5 (+5) CARGREEN 32·2 (+5)
Wet weather
Balanus crenatus
Lepralia Pallasiana
Arenicola marina
Sagartia luciae
Acartia bifilosa
NEILLE POINT BUOY. 33·2 (+5)
Littorina littorea
Leander squilla
Peloscolex benedeni
Actinia equinum
Sertularia pumila
Halichondria panicea
Acartia clausi
Ophiothrix fragilis
SALTASH BRIDGE 33·4 (+4½)
Eurytemora affinis
No. 15 BUOY 33·1 (+4½)
off Bull Point
Chthamalus stellatus
Eupagurus bernhardus
OFF CREMYL 35·2 (-2½)
APPROXIMATE DISTANCE FROM SEA, MILES
SALINITY
0
10
20
30
40
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18

FIG. 1.

size of the various springs and neaps, since the amount of salt water coming up was not the same at two corresponding phases of the tidal month. However, this can be neglected, as the intention was to obtain merely an approximate idea of the salinity of the stream.

The high-water salinity curve (Fig. 1) shows a gradual fall as far as Cargreen, after which there is a rapid decline to Weir Quay, about $1\frac{1}{2}$ miles further up. From there to Pentillie, round the two bends, the fall is again gradual, while from Halton Quay it increases until there is again a marked drop between North Hooe and Calstock, a distance of about 2 miles. Above Calstock, to Weir Head where the fresh water is met, the fall per unit distance appears to decrease towards the upper limit of the tidal region. Determinations of low-water salinity indicate that the greatest variation between low- and high-water concentrations is found between North Hooe and the Weir Quay district. As will be noticed later, this is the region where a large number of marine species reach their limit of existence.

Indications of the movement of sea-water were also seen in the distribution of marine plankton. There was a rapid reduction in the variety of species in passing from the junction of the Lynher and the Tamar to the junction of the Tamar and the Tavy. From this latter region upwards there were few species, the chief being *Sagitta bipunctata*, *Euterpina acutifrons*, and *Aurelia aurita*, which were found to have their upper limit about half-way between Pentillie Quay and Halton Quay. Along this length, as is mentioned above, there is a marked fall in the salinity about high water. Similarly there is a reduction in the number of bottom species. It would appear that the main body of incoming sea-water does not pass Cargreen. A considerable portion goes into the Lynher and the Tavy and covers the mud-flats on each side between Saltash and Neille Point. A further large quantity is held over the flats between Neille Point and Hole's Hole.

During observations at Calstock, July 11–13, with hot dry weather, there was a scum of unicellular algæ covering the river and exposed banks at low water. This extended downwards for about three-quarters of a mile. With the incoming of the tide, this scum was pushed upstream, almost unbroken, until it lay, at high water, along a length of about $1\frac{1}{4}$ miles immediately below Weir Head. Here the salinity was low, varying from $0{\cdot}06‰$ to about $0{\cdot}3‰$, and the mass of water was evidently largely derived from that portion which, at low water, extended down to the Cotehele locality. The place of this water would be taken by that pushed up from the lower region down to the Halton Quay–Pentillie Quay neighbourhood. This is suggested after a consideration of the low-water salinities at the places named. Support is added by results obtained at a point off Markwell, about 1 mile above St. Germans

Bridge, where indications of movement of water were obtained, as follows :—

2 p.m. salinity 1·7°/₀₀
2.30 p.m. ,, 1·7°/₀₀
3.20 p.m. ,, 1·9°/₀₀ first indication of flow.
3.50 p.m. ,, 2·4°/₀₀
4.10 p.m. ,, 10·7°/₀₀

Reference will be made later to these data, when the movements of organisms are considered.

The influence of wet weather on the salinity of these rivers has not been studied, but a sample at Cargreen showed a fall from 32·2°/₀₀, during dry weather, to 21·5°/₀₀ on a fine day but after a rainfall of 2·14 inches during the previous 7 days.* Both samples were taken at 5 hours of flow.

Few salinity determinations have been made in the River Lynher, but the results show that the concentration at high water, as far as Sheviock Wood, is quite high, 31·6°/₀₀ at 3½ hours' flow. About St. Germans and Port Eliot there was a very abrupt change in salinity from low water to high water, as is indicated above, when the tide begins to flow strongly. Here the number of species is small.

The interesting shore plants, which have been noticed, are *Fucus vesiculosus*, *Atriplex portulacoides*, and *Phragmites communis*. They extend to about North Hooe, Fucus and Atriplex upstream, and Phragmites downstream. The two latter meet about North Hooe, with a well-defined junction, while Fucus suddenly ceases. The seaweed is very poorly grown from Pentillie upwards, the vesicles and fronds being dwarfed.

The Collection of Organisms.

Besides the usual methods employed in shore-collecting and the use of the fine tow-net, the plankton-net devised by Russell (**41**) was found to be very efficient in taking the larger plankton. The net used was of stramin, and had a mouth of rectangular shape 3 feet by 9 inches. This was attached to an Agassiz frame 1 foot high, having two posterior bars 9 inches apart to which the mouth of the net was lashed. The mouth of the net was thus about 1½ inches from the bed of the stream when the frame was resting on the bottom. The nature of the ground rendered unnecessary the provision of a protecting outer bag. On the mud-banks and on the hard ground the apparatus worked very satisfactorily, but tended to dig up the beds of "Point-stuff." It was also used at various depths while the boat was anchored, the net being suspended against the

* Plymouth rainfall.

tide. In order to sample at definite depths, an extra bridle was attached to two "eyes" at the back of the frame, and when the whole apparatus was lifted by this bridle, the frame and net hung down so that the mouth was quite efficiently closed.

Generally it was quite sufficient to make collections in this way while the boat was at rest, but when the tide slackened, at high or low water, towing was necessary.

Faunistic Notes.

Species belonging to various parts of the Animal Kingdom have been taken from the two rivers. They fall into a number of groups in so far as their distribution is concerned, viz. :—

1. Those coming in from the sea, either planktonic or benthic, which are intolerant of the changing conditions, and disappear rapidly, especially between Neille Point and Weir Quay.
2. Those coming in from the sea tolerant of considerable change in conditions, and persisting (a) to Halton Quay–North Hooe, (b) to Calstock district.
3. Brackish-water species, which replace some of the marine species. These appear between Pentillie and Hole's Hole.
4. Freshwater species tolerant of slight salinity.

By far the greatest number falls into Group 1, a very much smaller number into Group 2, Group 3 is also small, while only two, *Tubifex tubifex* and *Sphærium casertanum*, have been found in Group 4.

In considering the distribution of the various species, notice must be taken of the local variations in the conditions which determine their presence or absence. Sessile organisms requiring a solid substratum are not normally found on the mud-banks. The occurrence of odd specimens of *Cereus pedunculatus* attached to occasional small stones, and of *Metridium senilis* and *Sagartia troglodytes* living on small pieces of wood on mud-flats, shows forcibly the dependence of such animals upon suitable substrata. The distribution of burrowing animals is also partly dependent upon the nature of the substratum, those requiring tough mud being rarely found in very soft deposits. Generally speaking the latter type of sediment has been found to carry an exceedingly scanty macrofauna.

The channels scoured by the strong tides are poorly populated by sessile organisms, except when there is a solid bed, such as a rock exposure or a piece of masonry. Occasionally Fucus obtains a foothold in a sandy bed, and the fronds may carry Polyzoa and Hydroids, along with a number of Harpacticids.

It is to be noticed that the fauna so far recorded consists, chiefly, of littoral species which are adapted to withstand the rapidly varying circumstances of estuarine life. The largest number of plankton species is found in the most saline region, while the brackish water has only a very few species.

Protozoa.

This part of the animal kingdom has not been studied and *Polystomella crispa* only has been recorded. It is very common in the more saline part of the river.

Porifera.

The sponges have been found to be limited to the water which is highly saline at high water, not extending at most beyond Cargreen. There is a great development of *Halichondria panicea* on the mussel-bed off Neille Point. The low-water spring-tide depth at this place was about 12–15 inches, and the bed was not observed ever to be exposed. Dr. G. P. Bidder, to whom I am indebted for its determination, describes it as of the estuarine metamp.

Cœlenterata.

Obelaria gelatinosa is the dominant marine cœlenterate, it being present in great quantity, especially below half-tide mark. After Hole's Hole it becomes more scanty and dwarfed, while its vertical extent becomes limited to low-water mark. *Obelia geniculata* has a very much more restricted range, not having been found past Weir Quay (Sal. H.W. about $25°/_{oo}$,$+\frac{1}{4}$ hr. $18{\cdot}8°/_{oo}$).

The gymnoblastic hydroids lie in two groups, *Clava squamata* and *C. multicornis*, which are the marine types disappearing past Cargreen, and *Cordylophora lacustris*, a brackish-water species living in the upper part of the stream, from about New Quay down to the neighbourhood of Halton Quay. The salinity range is extensive, varying, at high water, from about $0{\cdot}1°/_{oo}$ above Calstock to about $22°/_{oo}$ near Halton Quay. The densest growth is on Calstock Bridge and on the rocks at Ashburton Turn, where the vertical extent is up to half-tide. Towards the extremes of the Cordylophora region the vertical range becomes reduced to low-water mark.

The upper end of the range of *Obelaria gelatinosa* overlaps the lower end of that of Cordylophora.

None of the Anthozoa has been found where the high-water salinity is normally less than $33°/_{oo}$.

Aurelia aurita breeds extensively in the asexual stage on the mussel-bed off Neille Point. The medusæ regularly invade the river during the summer months, and have been taken up as far as near Pentillie Quay.

Nemertini.

Lineus ruber has been taken most commonly. None has been found in water having a high-water salinity of less than about 33°/₀₀.

Annelida.

The class Polychæta provided the largest number of species in this phylum, most of them disappearing before Cargreen or when the salinity began to fall rapidly about this region. The most numerous and widely spread species found were *Nereis diversicolor*, *Polydora ciliata*, *Heterocirrus zetlandicus*, and *Heteromastus filiformis*. *Arenicola marina* occurs in the more saline area, and especially in the Lynher up to Ince Castle and in St. John's Lake. It soon disappears when the salinity begins to fall. The last specimens seen in the Tamar were at Cargreen. *Kefersteinia cirrata* and *Magalia perarmata* are common on the Neille Point mussel-bed, but extend very little further. The widest range is that of *Nereis diversicolor*, which persists into a region with a tidal variation of about 7·8°/₀₀ salinity at high water to about 0·4°/₀₀ at low water. It is extremely abundant in the stiffer muds, and at all levels where the banks slope gently into the main channel. Where there is an abrupt slope into the main channel, the animal is usually absent below half-tide mark, the deposit here being sandy. Above half-tide mark the sediment rapidly becomes fine, so as to produce a substratum in which the worm can easily burrow.

Polydora ciliata has been found as far up as a region having a tidal salinity variation of from about 20°/₀₀ to 4°/₀₀. Although, in the Saltash district, it has been taken chiefly from its normal habitat, shells, in other places it has been found living in mud, and very commonly in mud tubes constructed in narrow cracks in rock. During the summer the plankton, from as far up as North Hooe, was found to contain large numbers of the larvæ of Polydora.

Of the Oligochæta, *Tubifex costatus* and *Clitellio arenarius* have a range similar to that of *Nereis diversicolor*. They are both abundant in the stiffer mud and beneath stones in muddy places. *Peloscolex benedeni* is associated with them until the salinity begins rapidly to fall. *Tubifex tubifex* extends from the fresh water into the upper brackish region. It may be regarded as succeeding *T. costatus*.

Crustacea.

The Cladocera are recorded only from the highly saline area.

Of the *Copepoda Gymnoplea* the species of greatest interest are *Acartia Clausi*, *A. bifilosa*, and *Eurytemora affinis*. *A. Clausi* is abundant in the

Hamoaze, diminishing in numbers above Saltash and finally disappearing about the confluence of the Tamar and the Tavy. *A. bifilosa* makes its appearance about this point, becomes numerous about Hole's Hole, and disappears somewhere near the Cotehele district. It has not been seen in the plankton from Calstock. *Eurytemora affinis* is scarce in the Saltash area, increases by Hole's Hole, forms the greater part of the plankton upwards along the river, until at Calstock it is present as almost a pure culture. Shortly after this point the numbers fall off rapidly, disappearance taking place near Morwell Rocks.

The salinity range at high water for *E. affinis* was determined to be approximately $33^{\circ}/_{\circ\circ}$ to $0{\cdot}1^{\circ}/_{\circ\circ}$.

The brackish-water Gymnoplea were found to be much more numerous at the beginning of November than at any other time during the summer, there being indications of an autumn–winter maximum. The adult females were all carrying eggs, and an enormous number of larvæ and young adults were found. It is noteworthy that, in a series of collections made between Neille Point and Morwell Rocks (7.11.28), the samples from the upper part of the river contained only adults with all the females carrying eggs, while those from the lower portion contained many larvæ and young adults, and relatively fewer egg-bearing females.

The Harpacticidæ are mostly littoral species, and do not appear to extend beyond a lower salinity limit of about $20^{\circ}/_{\circ\circ}$ at high water. The weed on the buoys in the Hamoaze and off Neille Point carries a very dense fauna, consisting chiefly of *Idya furcata*, *Thalestris longimana*, and *Parathalestris Clausi*. *Notodelphys Allmani* is coextensive with its host *Ascidiella aspersa*, which is restricted to the region of high salinity.

The distribution of the four species of *Cirripedia Thoracica* shows *Chthamalus stellatus* to have the narrowest range, *Balanus balanoides* and *B. crenatus* extending further up, but being restricted to a lower salinity limit of about $33^{\circ}/_{\circ\circ}$, and *B. improvisus* occurring furthest up in the region of great salinity variation, between low and high water.

In the up-river localities there were indications that additions to the barnacle population were made very occasionally since, at Cargreen, above Halton Quay and at St. Germans Bridge, there were no examples seen which could be regarded as having been deposited this year. All the specimens were very large, and apparently aged. During the summer, large numbers of Balanus nauplii from 5–12% of the total catch, were taken in the region of the mouth of the River Lynher, but none was seen in collections made off Neille Point.

Sacculina carcini has a limited distribution. No specimens of infected *Carcinus mœnas* were taken above Neille Point. The nauplii were very abundant in plankton taken in the Hamoaze, but none appeared to get up to the Neille Point district.

The Schizopoda contributed four species, of which *Schistomysis ornata* had the shortest range and the least significance from the point of view of number. The most abundant Mysid was *Neomysis vulgaris*, *Macropsis slabberi* was somewhat less, on the whole, and *Praunus flexuosus* much less than either. Neomysis and Praunus were usually found at or near the bottom, feeding on detritus. Of the mobile organisms the Mysids may be regarded as of the utmost importance in the conversion of detritus into animal matter. This importance, in the estuaries, can hardly be exaggerated.

Macropsis is usually found swimming freely in the more open water, and may be considered as a pelagic animal. Collections at different depths showed generally that it was most abundant in the upper portion of its vertical range, and was only occasionally taken within 1 foot of the bottom. On the other hand, Praunus and Neomysis were almost always thick within 1 foot of the bottom, and either absent or very poorly represented higher up. In shallow water, of about 1 fathom or less, the three species would be found well mixed down to the bottom. Occasionally, as when much fresh water was coming down, Neomysis and Praunus were taken near the surface. At such times there was a fair amount of turbidity.

The Mysids in the estuaries are moved about very much by the tide. Observations above St. Germans, near Markwell, gave the following data, collections being made with the stramin net resting on the bed, 10-minute hauls, in a stream, at most, 1 foot deep, the net being placed mouth upstream :—

	1.30 p.m., a few minutes before L.W.	2.40 p.m., during L.W. period.	3.25 p.m. after 10 mins. flow.
Neomysis vulgaris . .	40	10	6970
Crangon vulgaris . .	11	—	4
Gammarus locusta . .	1	1	1

Reference to the notes on salinity changes at this place (p. 86) will show that the rise in salinity commenced after 3.20 p.m., and was very marked at 4.10 p.m. As the water moved upstream the swarms of Mysids could be seen, in the shallow water along the edge, to form a thick soup, and the water surface here was bespattered with splashes, caused by the jumping of the myriads of overcrowded animals. This phenomenon was observed regularly, at the turn of the tide and for some time afterwards, until they were more thinly distributed over the substratum. A similar concentration takes place along the edge of the tide, as it ebbs from the mud-banks.

It is noticeable that the Mysid fauna at the edge of the tide is, in effect, a Neomysis fauna. The vertical distribution of Neomysis and Macropsis,

in the deeper parts, may be fairly generally expressed by the following table :—

Off Sheviock Wood R. Lynher.	2 ft. deep. % of total.	7 ft. deep. % of total.	13 ft. deep. % of total.	20 ft. deep. % of total.	Bottom 24 ft. % of total.
Macropsis slabberi	98·5	29	67	64	—
Neomysis vulgaris	—	8·4	18	14·2	47
Praunus flexuosus	—	43	4	—	—
Crangon vulgaris	—	—	—	—	27

The table does not show the usual distribution of Praunus, but in all other collections, whether singly from the bottom or in vertical series, this animal has been taken chiefly within the lowest foot or so of the bed. It and Neomysis are to be taken in great numbers among Fucus.

The three species are capable of suffering a very wide range of salinity changes ; especially is this the case with Neomysis, which extends from the sea up to Morwell Rocks, with a high-water salinity of about $0{\cdot}1^{\circ}/_{\circ\circ}$. The other two do not persist far beyond Calstock, where the high-water salinity was $7{\cdot}8^{\circ}/_{\circ\circ}$ and low-water $0{\cdot}3^{\circ}/_{\circ\circ}$.

Neomysis was observed breeding throughout the summer and into November, while Praunus and Macropsis were not taken with full brood-pouches later than the beginning of September.

Three species of Isopoda claimed special attention, viz. : *Sphæroma serratum*, *S. rugicauda*, and *Paragnathia formica*. The first is a marine species, which extends up the Tamar to about half-way between Hole's Hole and Pentillie Quay, where the high-water salinity was $24^{\circ}/_{\circ\circ}$; *S. rugicauda* succeeded it and persisted to a region a little above Calstock. The same succession was observed in the Lynher, the junction of the two ranges being near Sheviock Wood. *S. rugicauda* was found almost at the upper limit of the tidal zone, near Tideford. This species provided examples having one to three notches on the postero-lateral border of the exopodite of the uropod, collected at Calstock and St. Germans.

Paragnathia formica was also common in both rivers. In the Tamar, the determined range was from Neille Point to a piece of hard ground opposite the hamlet of Boheterick, a little distance below Calstock, with a high-water salinity of well below $20^{\circ}/_{\circ\circ}$. It was collected from the edge of salt marshes near high-water mark, in circumstances such as were described by Omer-Cooper (**36**), and from beneath stones at about half-tide. The praniza stage was often taken in the stramin net at various depths.

The *Amphipoda* have presented interesting examples of species range and succession.

Three species of Gammarus have been taken commonly, *G. marinus*, *G. locusta*, *G. duebenii*. The first was found to be co-extensive with *Fucus*

vesiculosus, and was not found further up than North Hooe. *G. locusta* was found to be very common and extended up to Morwell Rocks. *G. duebenii* was met with first opposite Cotehele Woods, below Calstock, and was common up to Weir Head, where the water was apparently fresh (H.W. Sal. 0·06°/$_{oo}$). It was abundant in the moss *Eurhynchium rusciforme*.

G. marinus was usually found among Fucus and under stones, *G. locusta* was also taken swimming freely, chiefly near the bottom, and was very abundant, in company with Neomysis and Praunus, on the banks of vegetable debris ("Point-stuff"), which formed at bends. *G. duebenni* was taken in similar circumstances to those of *G. locusta*, and may be regarded as succeeding the latter in brackish water.

Corophium crassicorne extends from the sea to about half-way between Cargreen and Weir Quay, where the salinity undergoes a considerable fall. It is very abundant among the weed growing on buoys in the Hamoaze and further upstream, and along the shore. *Corophium grossipes* succeeds it in the upper part of the stream, it having been met with first near North Hooe. This species burrows in the earthen banks and in the stiffer mud, and forms U-shaped earthen tunnels under stones. In the Calstock district it is very abundant and replaces *Nereis diversicolor* in the banks. A similar relation between the worm and the amphipod was seen in the River Tiddy, between St. Germans and Tideford. The upper limit was not discovered in the Tamar, but in the Tiddy it was coincident with the end of the tidal zone.

Seven species of Decapoda were recorded of which six may be considered. The genus Leander provided three species, viz., *L. serratus*, which extends almost up to Pentillie Quay, it being most abundant in the region of higher salinity, and is commercially exploited about Saltash and the lower district; *L. squilla*, which was not taken above Neille Point, but probably extends somewhat further, since it was common at this place; and *L. longirostris*, which occurs frequently in the Lynher and Tiddy, and in the Tamar above Hole's Hole, extending as far as about a mile above Calstock. A few juvenile specimens of this last species were taken in St. John's Lake. Gurney (**18**) records the taking of young stages of this species off Plymouth. *L. serratus* and *L. squilla* are also common in the Lynher.

Palæmonetes varians has been found abundantly about St. Germans, both in pools on the salt marsh, and in the side streams communicating with the river. It was taken also in the Tamar, a little above Calstock. On the whole, this species is much less abundant in the main stream than in the small lateral diverticula. It thrives well in a salinity change of from less than 0·3°/$_{oo}$ to 29·6°/$_{oo}$.

Crangon vulgaris and *Carcinus mænas* have a range about the same

as that of *Nereis diversicolor*, and are both common. In the upper portion of the Tamar, about Calstock, they appear to be smaller than nearer the sea. Large numbers have been taken from the beds of "Point-stuff," in company with Neomysis, Praunus, and *Gammarus locusta*.

Mollusca.

The common molluscs are few in species. In spite of the fact that there is a considerable amount of rock exposed within the observed range of *Patella vulgata*, this species has been found only rarely. *Littorina littorea* and *L. obtusata* are both common as far as Sheviock Wood and Neille Point, on both hard and soft ground. Old dead shells of *L. obtusata* were picked up beside Cargreen, but no signs of living examples were seen. The egg-capsules of *L. littorea* were taken in the plankton, half a mile above St. Germans Bridge. *Paludestrina stagnalis* was found swarming over the mud-flats which carry Zostera, viz.: St. Germans Lake and the flat next above Saltash Bridge, on the left bank. Its numbers diminish rapidly past Cargreen and it is found only occasionally above Pentillie. *Mytilus edulis* and *Cardium edule* have a commercial value about Saltash, many being collected up as far as Warren Point on the left bank, and Neille Point on the right. The mussel-bed off the latter point is quite extensive, lying in water from 12 inches to 18 inches at low tide. *Ostrea edulis* has been taken from the mussel-bed, and is said to be abundant in the vicinity. *Scrobicularia plana* is the only other mollusc which has been taken commonly. It is found in the stiff mud of St. John's Lake, of the Lynher as far as Port Eliot, and in the Tamar as far as Pentillie. It tends to decrease in number as the mud becomes softer or more sandy, and also as it is followed into the less saline waters.

Polyzoa.

Membranipora Lacroixii and *Bowerbankia imbricata* were taken up as far as half a mile above Halton Quay, where the salinity range from high to low water was approximately 21°/$_{oo}$ to 4°/$_{oo}$. The latter species is exceedingly abundant as far up as Cargreen, covering the Fucus fronds, in some cases, almost completely. Membranipora is also common, especially on stones and shells. *Lepralia Pallasiana* and *Alcyonidium mytili* both cease a little way beyond Cargreen, where the high-water salinity begins rapidly to decrease. They also are very abundant.

Tunicata.

Oikopleura dioica moves with the tide and does not appear to pass Saltash. *Ascidiella aspersa* is the common species, it being very abundant

on the mussel-bed off Neille Point, and becoming rapidly scarcer until it ends about Hole's Hole in the Tamar, and about Sheviock Wood in the Lynher.

Pisces.

For the purpose of these notes only *Gobius microps* will be considered here. It is present in great quantity and ranges up to Morwell Rocks. At Calstock it formed in three samples, taken with the stramin net, 10·4%, 15%, and 25% respectively of the total (29.6.28). Large numbers are to be found, at low water, in the small channels traversing mud-banks, and in pools. Along the edge of the tide, immediately after the Mysids have passed, they may be taken in abundance. When the mud-flats are covered by the tide, Gobius spreads out over the bed similarly to Neomysis and Praunus, but not in such quantity. It feeds chiefly upon Mysids and Copepods, and is to be regarded as a serious competitor of the young Clupeoids which live in the estuaries (**15**).

I wish to record my indebtedness to Dr. E. J. Allen, F.R.S., and the staff of the Marine Biological Laboratory, Plymouth, for valuable assistance and continued interest, to Dr. G. P. Bidder, Miss S. L. Garstang (Mrs. A. C. Hardy), Mr. W. Edgar Evans, Mr. R. Gurney, and Professor W. M. Tattersall, who have decided certain species for me, and to the Council of the University of Leeds who gave me leave of absence to carry out the investigation.

Note on Heterocirrus zetlandicus.

The worm which is recorded here under this name, although answering in most of its characteristics to the description of the species, differs from the type in not possessing crochets. All the setæ are capillary bristles, but in cases where they are broken the stumps have a resemblance to those figures of crochets given in Southern, Clare Island Survey, Proc. Roy. Irish Acad., XXXI–2, 1914, Pl. XII, Fig. 29 J.K. It agrees closely with stage B, *loc. cit.*, pp. 47, 117, 118, and the possibility suggests itself that the crochets described and figured by Southern were broken capillary bristles, damaged either recently or at a more remote period.

Faunistic List (Compare with lists in **1**, **2**, **3**, **37**, **38**).*

PROTOZOA Foraminifera :

Polystomellinæ

Polystomella crispa L. (**53**). Common in Tamar ; taken up to ½ mile above Cargreen. Common among tow-nettings and dredgings.

* Figures in thick type refer to the list of References on p. 107.

METAZOA Porifera :

Haplosclerida.

Halichondria panicea Pallas (**6**). Rat Island and Hamoaze ; massive growth on Neille Point mussel-bed.

Axinellidæ.

Hymeniacidon sanguineum Grant (**6**). Rat Island ; Weir Point.

Gymnoblastea.

Clavidæ.

Clava multicornis Forskål (**4**). Occasional, on wood and stones in main channel off Cargreen.

Clava squamata O.F.M. (**4**). Relatively common in main channel off Cargreen.

Cordylophora lacustris Allman (**4**). Abundant above, at, and below Calstock ; massive growth on Calstock Bridge, and on rocks below Cotehele Woods. Extends down to within $\frac{1}{2}$ mile of Halton Quay.

Calyptoblastea.

Campanulariidæ.

Obelia geniculata L. (**22**). On Fucus, as far as Cargreen in Tamar, and hard ground, by boathouse near Ince Castle in Lynher.

Obelaria gelatinosa Pallas (**22**). Abundant in Tamar, extending to North Hooe ; abundant in Lynher, extending to Port Eliot.

Gonothyraea Lovéni Allman (**22**). On Fucus near Warren Point, R. Tamar ; on Fucus near boathouse by Ince Castle, R. Lynher.

Sertulariidæ.

Sertularia pumila L. (**22**). On Fucus up to Neille Point, and to boathouse by Ince Castle.

Eucopidæ.

Phialidium hemisphaericum Gronovius (**29**). Taken in plankton up to within 1 mile of Pentillie Quay, R. Tamar, and up to Sheviock Woods, R. Lynher. Very abundant in Hamoaze and adjacent waters during summer.

Discomedusæ.

Ulmaridæ.

Aurelia aurita Lamarck (**29**). Medusæ taken to within 1 mile of Pentillie Quay, R. Tamar ; Scyphistomæ abundant on Neille Point mussel-bed, also at Cargreen Hard, and above Antony Creek, R. Lynher.

ZOANTHARIA.

Actiniidæ.

Actinia equina L. (**17**). On Rocks up to Neille Point, R. Tamar; up to boathouse near Ince Castle, R. Lynher.

Metridium senilis L. var. *pallidum* (**17**). On piece of wood ½ mile above Saltash Bridge.

Sagartia luciæ Verrill (**30**). On rocks at Bull Point, Hamoaze; Neille Point and Cargreen Hard, R. Tamar.

Sagartia troglodytes Gosse var. *ornata* (**17**). On piece of wood, ½ mile above Saltash Bridge; mussel-bed off Neille Point, R. Tamar.

Cereus pedunculatus Pennant (**17**). Rat Island; St. John's Lake.

Diadumene cincta T. A. Steph. (**51**). Mussel-bed off Neille Point, R. Tamar.

NEMERTINI.

Amphiporidæ.

Amphiporus lactifloreus Johnston (**25**). Under stones, between Saltash Bridge and Warren Point.

Tetrastemmidæ.

Prostoma melanocephalum melanocephalum Johnston (**8**). Under stones, between Saltash Bridge and Warren Point; Rat Island.

Lineus bilineatus Renier (**8**). Mussel-bed off Neille Point.

ROTIFERA.

Synchæta gyrina Hood (**34**). Common in plankton between Neille Point and Cotehele (Nov.).

POLYCHÆTA.

Syllidæ.

Syllis gracilis Grube (**12**). Rat Island.

Syllis prolifera Krohn (**12**). Bull Point, Hamoaze; mussel-bed off Neille Point.

Odontosyllis ctenostoma Claparède (**12**). Mussel-bed off Neille Point.

Exogone gemmifera Pagenstecher (**12**). Shore, by boathouse near Ince Castle, R. Lynher.

Autolytus prolifer O.F.M. (**12**). In plankton from Hamoaze, off Bull Point.

Hesionidæ.

Kefersteinia cirrata Keferstein (**12**). Rat Island; common in mussel-bed off Neille Point.

Magalia perarmata Marion and Bobretsky (**12**). Common on mussel-bed off Neille Point; Cargreen Hard.

Aphroditidæ.

Lagisca extenuata Grube (**12**). Mussel-bed off Neille Point.
Harmothoë impar Johnston (**12**). Mussel-bed off Neille Point.
Pholoë minuta Fabr. (**12**). Cargreen Hard.

Phyllodocidæ.

Phyllodoce maculata L. (**12**). Rat Island.

Nereidæ.

Leptonereis glauca Clap. (**12**). Mussel-bed off Neille Point.
Nereis (*Perinereis*) *cultifera* Grube (**12**). Rat Island.
Nereis (*Hediste*) *diversicolor* O.F.M. (**12**). Dominant animal in mud-banks, extending to ½ mile above Calstock, and to about 1 mile below Tideford.

Nephthydæ.

Nephthys Hombergii Lamarck (**12**). Widely distributed in mud, up to Pentillie Quay, and to lower end of Sheviock Wood.

Glyceridæ.

Glycera alba Rathke (**12**). Rat Island, in mud.

Spionidæ.

Scolecolepis fuliginosa Clap. (**13**). Neille Point, in small pool.
Nerine foliosa Aud. et M-Ed. (**13**). Rat Island, in mud.
Pygospio elegans Clap. (**13**). Shore, by boathouse near Ince Castle.
Polydora ciliata Johnston (**13**). Widely distributed up to ½ mile beyond Halton Quay and to Port Eliot. In mud, in clefts in rock, and in shells of Ostrea and Balanus.
Polydora hoplura Clap. (**13**). Mussel-bed, Neille Point.

Cirratulidæ.

Audounia tentaculata Montagu (**13**). St. John's Lake ; Rat Island.
Cirratulus cirratus O.F.M. (**13**). Rat Island ; shore, by boathouse near Ince Castle.
Heterocirrus zetlandicus McIntosh (**13**). Common in stiff mud, up to Neillé Point ; Rat Island.
Streblospio Shrubsolii Buchanan (**13**). Occasional, in mud off Port Eliot, and up to ½ mile above Halton Quay.

Terebellidæ.

Lanice conchilega Pallas (**13**). St. John's Lake ; Rat Island ; shore, by boathouse near Ince Castle.

Ampharetidæ.

Ampharete Grubei Malmgren (**13**). St. John's Lake.
Melinna palmata (**13**). Wivelscombe Lake ; Rat Island.

Capitellidæ.

Heteromastus filiformis Clap. (**13**). Common in stiff mud, in R. Tamar up to Neille Point, and in R. Lynher up to Sheviock Wood.

Capitella capitata Fabr. (**13**). Rat Island ; shore, by boathouse near Ince Castle.

Arenicolidæ.

Arenicola marina L. (**13**). Up to Cargreen, and to confluence of R. Lynher and R. Tiddy.

Sabellidæ.

Dasychone bombyx Dalyell (**13**). St. John's Lake.

Serpulidæ.

Pomatoceros triqueter L. (**13**). Up to Hole's Hole, and to Sheviock Wood. Commoner nearer the sea.

Spirorbis spirillum L. (**13**). Off Neille Point on stones.

Spirorbis borealis Daudin (**13**). Rat Island on Fucus and stones.

Oligochæta.

Naididæ.

Chætogaster diaphanus Gruith (**31**). Among moss at Weir Head ; a freshwater species in company with brackish-water forms.

Nais elinguis Müller, Oerstedt. (**31**). In moss with Chætogaster.

Tubificidæ.

Tubifex costatus Clap. (**32**). Widely distributed and common in mud, and under stones on mud and muddy sand, up to $\frac{1}{2}$ mile beyond Calstock Bridge, and to mud-flats above St. Germans Bridge.

Tubifex tubifex Müller (**31**). Extending from fresh water down to about $\frac{1}{3}$ mile above Calstock. In R. Tiddy near Tideford.

Clitellio arenarius Müller (**32**). In stiff mud and muddy sand, and under stones, up to $\frac{1}{2}$ mile above Calstock Bridge, and to shore, by boathouse near Ince Castle.

Peloscolex Benedeni Udeken (**32**). Up to Neille Point and Port Eliot, in stiff mud and muddy sand. Common.

Chætognatha.

Sagitta bipunctata Quoy and Gaimard (**19**). R. Tamar. Occasional specimens in plankton, $\frac{1}{2}$ mile beyond Pentillie Quay.

Branchiopoda.

Podon intermedius Lilljeb. (**34**). In Plankton, up to Neille Point, and to Sheviock Wood.

Evadne Nordmanni Lovén (**34**). In plankton, off *Impregnable*.

Chydorus sphaericus O.F.M. (**26**). Near lower end of Weir Island, Weir Head, in water carrying brackish-water forms. A freshwater species.

COPEPODA.

Calanidæ.

Calanus finmarchicus Gunnerus (**44**). At mouth of Hamoaze.

Pseudocalanidæ.

Pseudocalanus elongatus Bœck (**44**). In plankton off *Impregnable*.

Centropagidæ.

Centropages typicus Kröyer (**44**). Up to mouth of R. Tavy.

Temoridæ.

Temora longicornis O.F.M. (**44**). Up to mouth of R. Tavy.

Eurytemora affinis Poppe (**16**). From about *Impregnable* to Morwellham Quay and to Port Eliot. Common in brackish water.

Eurytemora velox Lilljeb. (**16**). In shallow pool on salt marsh above St. Germans.

Parapontellidæ.

Parapontella brevicornis Lubbock (**44**). In Hamoaze off *Impregnable*.

Acartiidæ.

Acartia Clausi Giesbr. (**44**). Common in Lynher, and in Tamar up to Neille Point.

Acartia bifilosa Giesbr. (**16**). Common in Tamar from Neille Point to near Cotehele.

Cyclopidæ.

Oithona helgolandica Claus (**46**). Up to Neille Point and to Antony Passage. Common.

Cyclopina longicornis Bœck (**46**). Up to Saltash. Common.

Harpacticoida.

Longipedia minor Scott (**45**). Neille Point; Hole's Hole, amongst weed and on mud.

Ectinosoma melaniceps Bœck (**47**). Cargreen Hard.

Euterpina acutifrons Dana (**45**). In plankton, to Halton Quay.

Harpacticus chelifer Müller (**45**). In weed, on Neille Point buoy.

Harpacticus gracilis Claus (**45**). Up to Halton Quay and to Sheviock Wood, in plankton and on bottom. Common.

Harpacticus flexus Brady (**45**). Up to Hole's Hole. Common.

Alteutha interrupta Goodsir (**45**). On Neille Point buoy, and in tow-nettings from off Wivelscombe Lake.

Idya furcata Baird (**45**). Common on buoys and on shore, also in tow-nettings. Up to Hole's Hole, and boathouse by Ince Castle.

Thalestris longimana Claus (**45**). Up to Neille Point buoy. Common on buoys.

Parathalestris harpacticoides Claus (**45**). On No. 15 Buoy, Hamoaze.

Parathalestris Clausi Norman (**45**). On buoys up to Neille Point. Common.

Dactylopusia thisboides Claus (**45**). Rat Island; up to Neille Point buoy.

Dactylopusia vulgaris G. O. Sars (**45**). Neille Point, in pool at half-tide.

Dactylopodella flava Claus (**45**). Rat Island.

Laophonte proxima G. O. Sars (**45**). Cargreen Hard; Hole's Hole. On Bowerbankia.

Laophonte similis Claus (**45**). On shore, by boathouse near Ince Castle.

Laophonte Strömi Baird (**45**). Common on buoys up to Neille Point.

Laophonte abbreviata G. O. Sars (**47**). Half a mile above Cargreen, on mud.

Enhydrosoma propinquum Brady (**45**). In tow-nettings, off *Impregnable* and near Sheviock Wood.

Cymbasoma longispinosum Bourne (**48**). In tow-nettings, up to Sheviock Wood, and to Neille Point buoy.

Corycæidæ.

Corycæus anglicus Lubbock (**7**). In plankton, off *Impregnable*.

Notodelphydæ.

Notodelphys Allmani Thorell (**48**). In *Ascidiella aspersa*, up to Hole's Hole, and Sheviock Wood.

Ascidicola rosea Thorell (**48**). In *Ascidiella aspersa*, Sheviock Wood.

Cirripedia.

Balanidæ.

Balanus balanoides L. (**10**). Up to shore by boathouse near Ince Castle, and to Cargreen. Common.

Balanus crenatus Bruguière (**10**). Up to shore by boathouse near Ince Castle, and to Cargreen. Fairly common.

Balanus improvisus Darwin (**10**). Half a mile above Halton Quay; St. Germans Bridge.

Chthamalus stellatus Poli (**10**). Bull Point, Hamoaze.

Peltrogastridæ.

Sacculina carcini Thompson (**52**). On *Carcinus mænas* up to Neille Point.

SCHIZOPODA.

Mysinæ.

Praunus flexuosus Müller (**34**). Common up to ¼ mile above Calstock, and to ½ mile above St. Germans Bridge.

Schistomysis ornata G. O. Sars (**34**). Up to Sheviock Wood.

Macropsis Slabberi v. Beneden (**34**). Abundant. Up to ½ mile above Calstock, and 2 miles above St. Germans.

Neomysis vulgaris Thompson (**34**). Very abundant. Up to Morwell Rocks, and to Penimble, R. Tiddy.

ISOPODA.

Anthuridæ.

Anthura gracilis Montagu (**35**). Occasional. Rat Island; off Port Eliot. In mud.

Sphæroma serratum Fabr. (**49**). Up to 1 mile above Weir Quay, and to Wivelscombe Lake.

Sphæroma rugicauda Leach (**49**). From ½ mile below Pentillie Quay to ½ mile above Calstock; from Sheviock Wood to Tideford. Abundant.

Dynamene rubra Leach (**49**). Shore at Bull Point, Hamoaze.

Limnoriidæ.

Limnoria lignorum Rathke (**43**). In log, on mud-flat ½ mile above Cargreen.

Gnathiidæ.

Paragnathia formica Hesse (**33**). Neille Point to 1 mile below Calstock; about junction of R. Lynher and R. Tiddy and main stream. Common. Got from edge of salt marsh about H.W., and in tow-nets.

Janiridæ.

Jæra marina Fabr. (**43**). Common at Bull Point, Hamoaze; shore, by boathouse near Ince Castle.

Idotheidæ.

Idothea baltica Pallas (**43**). St. John's Lake among Zostera; off Ince Castle.

Ligiidæ.

Ligia oceanica L. (**43**). In rocks by Ince Castle; in wall above Saltash Bridge.

Cryptoniscinæ.

Hemioniscus balani Spence Bate (**52**). In *Balanus balanoides* from St. John's Lake and Bull Point.

AMPHIPODA.

Hyperiidæ.

Hyperia galba Mont. (**42**). One mile below Pentillie Quay, *Aurelia aurita* also taken.

Orchestiidæ.

Orchestia littorea Mont. (**42**). Up to North Hooe, and to Ince Castle.

Calliopiidæ.

Apherusa Jurinii M.Edw. (**42**). Corner opposite *Defiance*, right bank. Ovigerous females, and small half-grown animals (19.8.28).

Gammaridæ.

Gammarus locusta L. (**42**). Very common up to Morwell Rocks, and to Tredinnick, below Tideford.

Gammarus marinus Leach (**42**). Common to North Hooe, and to junction of Lynher and Tiddy.

Gammarus duebenii Lilljeb. (**42**). From about 1 mile below Calstock to Weir Head; from Sheviock Wood to Penimble, below Tideford.

Melita palmata Mont. (**42**). Up to Weir Quay, usually on hard ground.

Podoceridæ.

Podocerus (*Jassa*) *falcatus* Mont. (**42**). In weed on buoys, up to Neille Point and up to Sheviock Wood. Taken from bottom and in nets. Common.

Podocerus odontonyx G. O. Sars (**42**). No. 15 Buoy off Bull Point, Hamoaze. Fairly common.

Corophiidæ.

Corophium crassicorne Bruzel (**42**). Up to $\frac{1}{2}$ mile above Cargreen. Common on buoys and on mussel-bed.

Corophium grossipes L. (**42**). Common from North Hooe towards Morwellham; R. Lynher from Wacker Creek* to Tideford.

Caprellidæ.

Pseudoprotella phasma Mont. (**9**). Off lower end of Sheviock Wood, 1 specimen.

Pariambus typicus Kröyer (**9**). Off lower end of Sheviock Wood, 1 specimen.

MACRURA.

Palæmonidæ.

Leander serratus Pennant (**52**). Up to Pentillie Quay, and to confluence of Lynher and Tiddy. Common.

* Near Antony, after which the author has named it, *passim*.—Ed.

Leander longirostris H.M.-Ed. (**52**). From St. John's Lake to $\frac{1}{4}$ mile above Calstock Bridge. In Lynher to $\frac{1}{4}$ mile above St. Germans Bridge.

Leander squilla L. (**52**). Up to Neille Point, and to boathouse near Ince Castle.

Crangonidæ.

Crangon vulgaris L. (**52**). Up to $\frac{1}{4}$ mile above Calstock, and to $\frac{1}{4}$ mile above St. Germans Bridge. Common.

Anomura.

Paguridæ.

Eupagurus bernhardus L. (**5**). St. John's Lake ; Bull Point ; Hamoaze.

Porcellanidæ.

Porcellana longicornis L. (**5**). Mussel-bed, Neille Point.

Brachyura.

Portunidæ.

Carcinus mœnas Pennant (**5**). Common up to $\frac{3}{4}$ mile above Calstock Bridge, and to Tredinnick.

Insecta.

Thysanura.

Petrobius maritimus Leach (**39**). Up to Port Eliot, and to Warren Point.

Trichoptera.

Leptocerus annulicornis Steph. (**40**). Larvæ in moss, with brackish-water forms, below Weir Head. A freshwater larva.

Prosobranchiata.

Patellidæ.

Patella vulgata L. (**24**). Occasional specimens on stones, on mud-bank ; St. John's Lake, and left bank above Saltash Bridge.

Littorinidæ.

Littorina littorea L. (**24**). Common up to Neille Point, and to Sheviock Wood.

Littorina obtusata L. (**24**). Common up to Neille Point, and to Sheviock Wood.

Littorina rudis Maton (**24**). St. John's Lake , by boathouse near Ince Castle.

Assimineidæ.

Paludestrina stagnalis Baster (**24**). Common up to North Hooe, and to Sheviock Wood.

Cypraeidæ.

Trivia europæa Mont. (**14**). Mussel-bed, Neille Point, 1 specimen.

Pelecypoda.

Mytilidæ.

Mytilus edulis L. (**14**). Common up to Weir Quay, and to Sheviock Wood.

Scrobiculariidæ.

Scrobicularia plana da Costa (**14**). Common in stiff mud. Up to Pentillie Quay, and to Port Eliot.

Tellinidæ.

Macoma baltica L. (**14**). Shore, by boathouse near Ince Castle. Dead shells near Hole's Hole.

Veneridæ.

Tapes pallustra Mont. (**14**). Rat Island.

Cardiidæ.

Cardium edule L. (**14**). Common. Up to Hole's Hole, and to St. Germans.

Cycladidæ.

Pisidium casertanum Poli (**50**). In fine clean sand, down to lower end of Morwell Rocks. Freshwater species among brackish-water forms.

Polyzoa.

Membraniporidæ.

Membranipora Lacroixi Audouin (**23**). Common. Up to ½ mile above Halton Quay, and to St. Germans Bridge.

Escharidæ.

Lepralia Pallasiana Moll (**23**). Common. Up to Cargreen, and to Sheviock Wood.

Alcyonidiidæ.

Alcyonidium mytili Dalyell (**23**). Common. Up to ½ mile above Cargreen, and to shore, by boathouse near Ince Castle.

Vesiculariidæ.

Bowerbankia imbricata Adams (**23**). Very abundant. Up to ½ mile above Halton Quay, and to confluence of Lynher and Tiddy.

Pedicillinidæ.

Pedicillina cernua Pallas (**23**). Mussel-bed, Neille Point.

ECHINODERMATA.

Ophiothricidæ.

Ophiothrix fragilis Abildgaard (**27**). Mussel-bed off Neille Point.

TUNICATA.

Appendiculariidæ.

Oikipleura dioica Fol. (**34**). In plankton. Hamoaze up to *Impregnable*.

Molgulidæ.

Molgula manhattensis De Kay (**20**). St. John's Lake; lower end of Sheviock Wood. Occasional.

Ascidiidæ.

Ascidiella aspersa O.F.M. (**21**). Common. Up to ½ mile above Hole's Hole, and to Sheviock Wood.

Ciona intestinalis L. (**21**). Occasional. Shore, by boathouse near Ince Castle.

Botryllidæ.

Botryllus Schlosseri Pallas (**20**). Up to Hole's Hole on *Fucus*.

Botrylloides rubrum M.-Ed. (**21**). Rat Island.

Didemnidæ.

Distalpia sp. Shore, by boathouse near Ince Castle.

CYCLOSTOMATA.

Petromyzontidæ.

Petromyzon marinus L. (**11**). Weir Head.

PISCES.

Salmonidæ.

Salmo salar L. (**11**). In Tamar and tributaries.

Murænidæ.

Anguilla vulgaris Turton (**11**). Up to Weir Head.

Syngnathidæ.

Syngnathus acus L. (**11**). Up to Hole's Hole, and to Sheviock Wood.

Mugilidæ.

Mugil chelo Cuvier (**11**). Up to Weir Head. Common.

Pleuronectidæ.

Pleuronectes flesus L. (**11**). Up to Weir Head, and to Port Eliot.

Gobiidæ.

Gobius microps Kröyer (**11**). Very abundant. Up to Morwell Rocks, and to Port Eliot.

Agonidæ.

Agonus cataphractus L. (**11**). Mussel-bed, Neille Point.

Blenniidæ.

Blennius pholis L. (**11**). Rat Island.

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On some Factors Limiting the Habitat of *Arenicola marina*.

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INTRODUCTION.

In connection with a certain problem in Palæontology (**1**) it became necessary to learn in what manner the marine burrowing worms of the past (but not the tubicolous worms) were likely to have behaved with regard to red oxide of iron in the amorphous state. Some of the sands (now rocks) in which those worms burrowed contained a large amount of iron oxide, others contained practically none at all. Owing, however, to certain differences and one particular common feature shown by the rocks in question, the following experiments were instituted in the hope that the habitat of the present-day worms might throw some light on the conditions of the past.

Type of Habitat of *A. marina*.

Curiously enough, despite all that has been written about *A. marina* no accurate details can be found dealing with either the nature of the ground material nor with the minimum density of the water tolerated by the organism.

With regard to the minimum density Benham (**2**) says, "*A. marina* lives equally well in water of very different density," and Ashworth (**3**) states that it occurs far up certain estuaries which, in times of flood at

least, are of much less density than sea-water. He also quotes Bohn to the effect that the absence of *A. marina* from the northern parts of the Baltic may be due to the same cause.

The information dealing with the ground material is much more plentiful. The researches of Allen and Todd (**4**, **5**) in the Salcombe and Exe estuaries would seem to show that *A. marina* in that locality is confined to a ground material consisting of mud and sand, mud and gravel, but very seldom, if ever, occurring in pure sand or pure mud. Ashworth (**3**) simply says that, "all species of Arenicola burrow in sand or gravel." Ferronnière (**6**) in his exhaustive survey of the Loire Estuary says that *A. marina* is found in sand containing an admixture of mud, but not in fresh deposits of mud where the water is flowing, although they were found in fœtid mud. Here, I think it is necessary to draw some distinction between the different kinds of mud. Fœtid mud must contain some organic matter, while mud formed by silt may contain very little organic matter and can hardly ever become fœtid.

My own limited investigations have shown that Arenicola does not occur in very pure sand. Where such appears to be the case, digging almost invariably shows that the pure top layer overlies a bed of sand mixed with mud.

From the work of Davidson (**7**) it will be seen that the top layer of sand must be more or less purified since the worms pass vast quantities through their bodies annually and, in the process, remove the organic matter.

Material and Apparatus.

The material used in this work consisted of a number of specimens of *Arenicola marina* supplied by the Marine Biological Station at Plymouth, quantities of sea-sand and sea-water and the following substances in a very finely divided state which were not known to have lethal properties :—

Ferric oxide.
Calcium carbonate.
Magnesium carbonate.
Stourbridge clay.
Kaolin.
Kieselguhr.

The apparatus consisted of a number of wide-mouthed bottles of 150 c.c. capacity and several "gas jars," 10 inches high and 2 inches in internal diameter.

Aeration was effected by means of a filter-pump fixed to a water-supply tap and connected by rubber tubing via a 4-way pipe to the various jars.

The jars were fitted with rubber stoppers and two glass tubes. Aeration of the water was, therefore, caused by suction and not by blowing as is more usual. This method was found to be highly satisfactory and, by careful adjustment of the size of the pipes, no great head of water was necessary to ensure a constant supply of air.

A. Experiments with Ferric Oxide.

Three gas jars were used for this experiment. Each contained 300 gms. of fresh sea-sand and 250 c.c. of sea-water.

The control worm was placed in its jar (A1). It immediately burrowed into the sand where it remained throughout the course of the experiments.

To jar (A2) was added 2 gms. of ferric oxide. This was allowed to settle, and then, by means of a glass rod, was stirred into the sand to a depth of about one and a quarter inches. This layer represented about 1 gm. of the oxide to 50 gms. of sand. When this had stood for an hour and very little oxide remained in suspension a worm was introduced. It immediately showed every sign of discomfort, wriggling into knots and everting and introverting its pharynx.

It made no attempt to burrow other than to place its anterior extremity against the sand and remove it almost immediately. When its movements began to slacken in vigour the organism was removed from the jar and revived in pure sea-water.

Fifty grammes of fresh sand were then poured evenly over the top of the sand and oxide, the water was pipetted off and a fresh supply added, thus ensuring that there was practically no iron oxide in suspension nor in direct contact with the water.

The same worm was again introduced. At first it remained quite still, but soon it began to burrow. The burrow extended down vertically only as far as the surface of the layer of oxide when it tended to run parallel to it, but never pierced it.

Jar (A3). A specimen of *Arenicola marina* was placed in a jar containing sand with a layer of iron oxide overlaid with $\frac{3}{4}$ inch of pure sand. The worm immediately started to burrow. On reaching the oxide it withdrew from the sand. This burrowing down to the oxide and complete withdrawal on coming in contact with it occurred several times. Ultimately, however, the burrow was continued along the surface of the oxide.

After a time, since the worm showed no sign of piercing the oxide, it was removed and placed in a jar containing only pure sand and sea-water. It was noticed that a small amount of the oxide had adhered to the anterior end of the worm. At first it made no attempt to burrow, but after lying quiescent for about three hours (after which time the

oxide, although still there, was more in the nature of a layer of mucus containing iron oxide than a direct layer of the oxide on the worm), it burrowed completely.

Jar (A4). The conditions in this experiment were exactly similar to those in the previous experiment. Again the worm burrowed down to the surface of the oxide, but it did not withdraw from the burrow. After a certain amount of hesitation it continued the burrow parallel to the surface of the oxide. When no further effort was made to burrow vertically the worm was removed and placed in a jar of pure sand and sea-water. The anterior end of this worm had only a trace of oxide adhering to it. Burrowing commenced in just over an hour.

Jar (A5) was similar to (A1) in composition except that the sand contained 1 gm. of ferric oxide evenly distributed throughout. On top of this mixture a very thin layer of pure sand was spread. When a worm was introduced it almost immediately pierced the pure sand, but hesitated when it came into contact with the underlying mixture. However, after a few abortive attempts it ultimately burrowed right down until it was completely immersed. Its behaviour differed from that of the control in as much as while the control remained buried this specimen soon protruded its posterior end from the burrow and remained in that position until stimulated by tapping the jar or by shutting off and turning on the air supply suddenly. From these results it will be seen that *Arenicola marina* found the presence of ferric oxide repellent under two conditions only, viz. :—

1. When the water contained it in suspension.

2. When mixed with sand in a high proportion (1 gm. oxide to 50 gms. sand).

Since it appears to be more likely that Arenicola under natural conditions would come into contact with the ferric oxide in suspension in water, rather than the oxide-sand mixture, a further set of experiments were set going in order to find out the effect of the suspension on the worm.

To this end a suspension was made up of 0·5 gm. of the oxide in 100 c.c. sea-water. When a worm was introduced it immediately showed symptoms of acute discomfort in the usual way, i.e. by violent wriggling, etc. After six hours this worm ceased to show any movement and could not be revived.

B. Experiments with other Substances.

These results, of course, merely suggest that ferric oxide is abhorrent to Arenicola, so the following experiments were undertaken to find if the substance were lethal, and if so, in what quantity. The apparatus

used was essentially the same as formerly, except that wide-mouthed bottles of 150 c.c. capacity were used instead of jars.

Three such bottles were fitted up as follows : water 140 c.c., with

	Ferric oxide.	Worm, size.
B1	0·00 gm.	Medium.
B2	0·05 gm.	Large.
B3	0·03 gm.	Small.

Almost immediately after introducing the oxide to bottles B2 and B3 it had completely enveloped both worms in a thin layer, but with this difference, worm B2 had practically all the available oxide adhering to it while worm B3 had only a portion of the available oxide adhering to it, although it was as completely enveloped as B2. (This, of course, was owing to its smaller size.)

The oxide, it may here be explained, was caught and retained by the mucus secreted by the worm.

In the case of worm B2, after 20 hours, the movements of the organism caused the oxide-laden sheath of mucus to be formed into a band about 1 cm. wide towards the anterior end, and from this time onwards the worm began to revive.

B3, however, was not so happily situated. No sooner did the mucous sheath begin to shorten than the parts so exposed collected a further coat of the oxide not previously collected. This coat it did not survive.

From this it can be concluded that ferric oxide in the amorphous state is not necessarily an active poison as far as *Arenicola marina* is concerned, but that it is lethal only when it can form with the mucus secreted by the organism a coat to shut off contact with the surrounding water for a sufficiently long period, and so inhibit respiration.

The difference between the case of A3 and B3 (when A3 lived in sand containing 0·3% of the oxide in sand while B3 was killed by 0·021%) may be explained by the fact that by burrowing through the sand the layer of oxide is scraped off with the mucus used to support the walls of the burrow.

If, as has been said, ferric oxide is lethal only in virtue of its physical properties, other substances of similar physical properties ought to act in the same way towards Arenicola.

To this end the B group of tests were repeated in exactly the same manner with (1) Calcium carbonate, (2) Magnesium carbonate, (3) Stourbridge clay, (4) Kaolin and (5) Kieselguhr. The results were so near those got with ferric oxide that it would merely be repetition to give details of the individual results, although it was noted that the kaolin appeared to be more intensely irritating to the worm than any of the others.

At the suggestion of Dr. Orton (to whom I am deeply indebted) these experiments were repeated in order that any alteration in hydrogen ion concentration might be checked.

The original sea-water was pH 7·95. The hydrogen ion concentration at the end of the experiment was found to have increased in the case of the control to pH 8·05. At the death of the worms it was pH 8·15 except in the case of the calcium carbonate where it reached the maximum of pH 8·35.

These results seem to prove, therefore, that it is the physical form and not the chemical composition of the substance which the organisms find intolerable.

Degree of Salinity.

Although the foregoing results would seem to show that *Arenicola marina* is unlikely to be found living in places where a large amount of fine sediment is brought down in suspension, it was found desirable to secure some data as to the degree of salinity of the water which would be necessary for the life of the organisms in estuaries. In this connection the jars each contained 100 gms. fresh sand.

C1 was used as a control with pure sea-water. C2–C5 contained respectively diluted sea-water, 75%, 50%, 30%, and 20%.

After four days no difference could be detected between the condition of the worms in C1, C2.

C3 and C4, however, were very much less active and showed no inclination to burrow, although they moved about in a feeble manner.

C5 remained almost motionless except for very inconspicuous rhythmic contractions. The condition of the organisms (C3–C5) may best be described as of such extreme turgidity that they were quite unable to exercise any power of locomotion, so that as burrowing worms they had ceased to exist.

An attempt was then made to find to what extent *Arenicola marina* could be slowly acclimatised to reduced salinity. Sea-water of salinity 35·2‰ was used as standard (pH 7·95).

Three 150 c.c. bottles were used.

C6 . . Control.
C7 . . 50 pts. sea-water to 50 pts. fresh.
C8 . . Normal sea-water.

Ten c.c. distilled water was added every 24 hours at first, but owing to the condition of the worm less frequent additions were made towards the end. (On several occasions the bottles became too full and some of the mixture had to be poured off.)

C7 became rather turgid when placed in the mixture, but moved about

slightly. On the addition of more fresh water it practically ceased to move and only its turgid state indicated the condition of life. On the fifth day, however, it died—becoming quite flaccid—and the salinity was found to be 3·10‰ (pH 7·65).

C8 lived normally for the first four days after which, though never showing so much turgidity as C7, its movements slowed down and it died on the eighth day when the salinity of the water was 14·39‰ (pH 7·85).

While these experiments were going on the control worm of the previous experiment in its bottle was still being aerated, and at the same time evaporation was going on so that the salinity was gradually increasing. It was not noticed that the worm as a whole became any thinner or less active, but the effect on the caudal end was most marked. The latter did not become generally attenuated, but became reduced in length and constricted at three places, more or less equidistant, so that the part appeared as a series of knots. At the death of this worm (after evaporation had been going on for 12 days) the salinity was found to be 37·4‰ and the pH 8·05.

From C7 and C8, taken in conjunction with the previous lot of experiments, it would appear that *A. marina* does not tend to adapt itself to any great change in salinity, its range probably lying between 35‰ and 25‰ for, although it may actually live beyond those limits in the Laboratory, it could not do so under natural conditions.

Also, it should be noted that no sand was placed in the vessels with the worms during the latter experiments because of the fact that no guarantee could be given that the sand contained water of the same salinity as that above the sand.

SUMMARY.

In the foregoing work it was found that: *Arenicola marina* was repelled and could not burrow in sand containing 2·0% of ferric oxide in the amorphous state.

That 0·021% ferric oxide in suspension in sea-water was lethal owing to its forming with the mucus of the organism an envelope which prevented contact with the surrounding air-carrying water.

That calcium carbonate, magnesium carbonate, Stourbridge clay, kaolin, and kieselguhr had the same effect as the ferric oxide in suspension.

That although able to live for a short time in water of salinity 3·10‰, *Arenicola marina* tended to become so turgid in water of 14·32‰ as to be unable to burrow.

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Notes on the Rate of Growth of *Tellina tenuis* da Costa in the Firth of Clyde.

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With 5 Figures in the Text.

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I. Foreword.

The material on which the present paper is based was collected from the Millport Marine Biological Station. I am indebted to the Superintendent, Mr. Elmhirst, for facilities for making the collections.

The biology of *Tellina tenuis* in the Cumbrae and neighbourhood was investigated during the autumn of 1926 and in 1927 (**2**), and the present paper is a direct continuation of that work. On several points in the earlier work, especially on the rate of growth of the species, it was felt that confirmatory evidence was necessary. A comparison of the size-frequency curves for the autumn of 1926 and 1927 showed that while on the 1926 curve there were only two modes, there were three on the 1927 curve, and that the mid mode of 1927 fell midway between those of 1926. This meant either, that rate of growth of the intermediate group in 1927 had been only half of that of the corresponding group in the previous year, or that on the 1926 curve one or more year groups were unrepresented. The latter explanation was considered at the time to be the more satisfactory one, and the work of the present year seems to confirm that view.

In the earlier investigation samples were collected at five intertidal

stations, and at several stations below L.W.M., but for the present study it was not deemed necessary to re-examine all these, and regular collecting was restricted in the intertidal zone to Stations 5 and 2 (at L.W.M. springs and 40 yards below H.W.M. neaps respectively), and below L.W.M. to Stations 6 and 7 (2 and 3 fathoms respectively). In the earlier investigation the amount of sand sieved at the intertidal stations was a standard cut of a $\frac{1}{4}$ sq. metre dug to a depth of about 15 cm.,* but during 1928, in addition to this standard cut, extra cuts were sieved to increase the collections, especially for the older groups. For comparison with Kames Bay one station on the Hunterston Sands was examined. All stations were visited three times during the year, in March, June, and the end of September.

II. Rate of Growth at Stations 2 and 5.

Stn. 5 (Figs. 1–2. Table VI).

A comparison of the figures for October, 1927, with those of March, 1928, shows that, as in the previous year, there had been no growth during the winter months. There had been, however, a considerable mortality amongst the smallest individuals (1927 spat), the proportion of the population at 3 mm. having fallen from 20·7% to 14·8%.

By the beginning of June, 1928, only a little growth was apparent, the mode at 7 mm. having shifted to 8 mm. and that at 11 mm. to 12 mm., but there was no sign of any growth amongst the smaller sizes, the mode remaining at 3 mm.

By the end of September, 1928, the mode at 8 mm. in June had moved to 9 mm., but the group represented by the mode at 12 mm. in June, although still present, no longer formed a distinct group.

The greatest change had taken place amongst the smaller sizes in which the mode at 3 mm. in June had moved to 6 mm. and the young spat had appeared at 3 mm.

Compared with 1927 growth had been rather less and, amongst the smaller sizes, more erratic. For example, in 1927 the mode at 3 mm. in April moved to 5 mm. in June and to 7 mm. by the beginning of October, while in 1928 the mode at 3 mm. in March was still at the same figure in June, but reached 6 mm. by the end of September.

On the size-frequency curve for September, 1928, there are three modes at 3 mm., 6 mm., and 9 mm., representing respectively :

0+	group	1928 spat.
1+	,, ...	1927 ,,
2+	,, ...	1926 ,,

* Contracted in the rest of the paper to "$\frac{1}{4}$ sq. m."

as we know from measurements since September, 1926. On the curve for October, 1927, there were also three modes at 3 mm., 7 mm., and 11 mm. respectively, which were considered to represent the 1927 spat, 1926 spat, and 1924 spat respectively (2, p. 690).

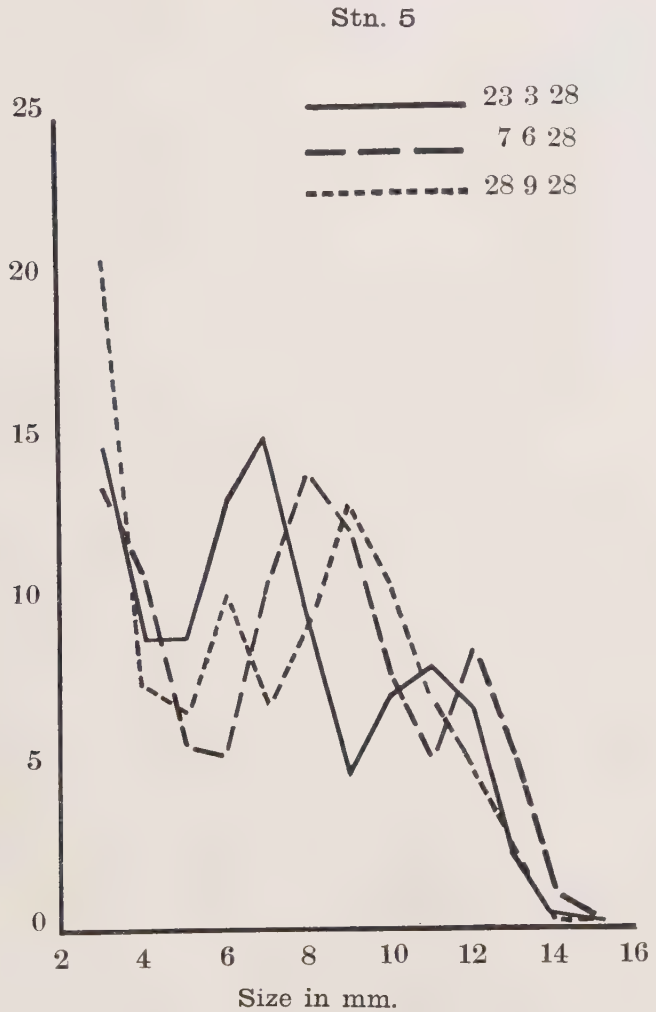

FIG. 1.—Graph showing the percentage (ordinate) of the catch at each mm. for Stn. 5 in March, June and Sept., 1928.

The view that a year group (1925 spat) was unrepresented on the curve for 1926 seems justified when we consider that the rate of growth during 1928 was of the same order as during 1927 and that there was in September, 1928, a mode at 9 mm., the figure at which, in the earlier paper, it was

considered that a year group should have been present on the curve for September, 1926 (2, p. 690).

The various year groups did not form equal proportions of the population. Since 1926 the spat of that year has continued as a dominant

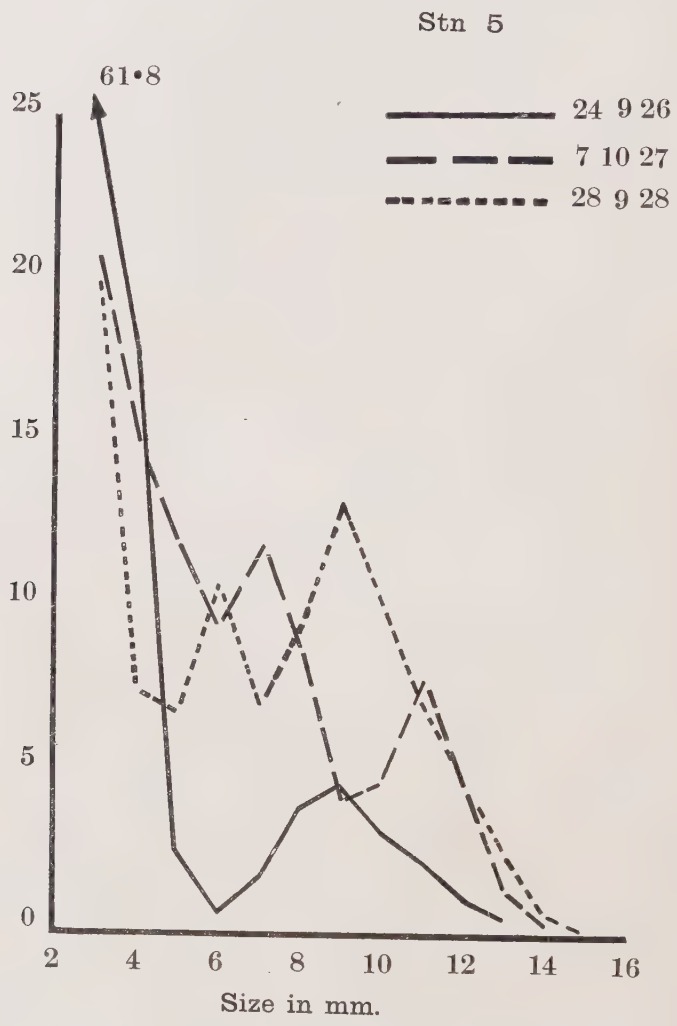

Fig. 2.—Graph showing the percentage (ordinate) of the catch at each mm. for Stn. 5 in Sept. 1926, Oct. 1927, and Sept. 1928.

group, and as the 2+ group in September, 1928, even with the natural rate of mortality of two years, it formed a large proportion of the population (Fig. 2). If we take the numbers from 8 mm. to 11 mm.

as representing the group, the proportion was 40% and the actual numbers per "$\frac{1}{4}$ sq. m." 304.

These figures also indicate that in Kames Bay the species can be subject to little interference, for it is unlikely that if this were to any extent a

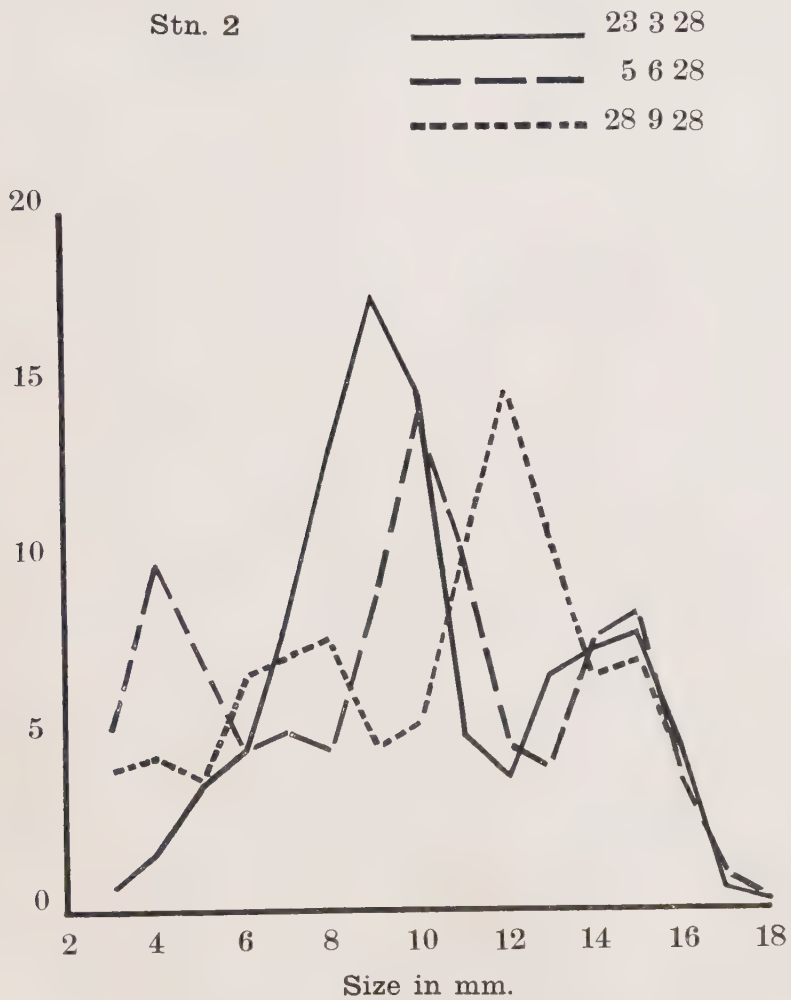

FIG. 3.—Graph showing the percentage (ordinate) of the catch at each mm. for Stn. 2 in March, June and Sept. 1928.

feeding-ground for fish the 1926 spat could have survived in such numbers.

STN. 2 (Figs. 3–4. Table VI).

As at Station 5, there was no growth during the winter months, the size-frequency curve for March, 1928, being very similar to that of October,

1927. Again, the maximum concentration of the individuals 3 mm. in length occurred in late spring, not in autumn as at Station 5.

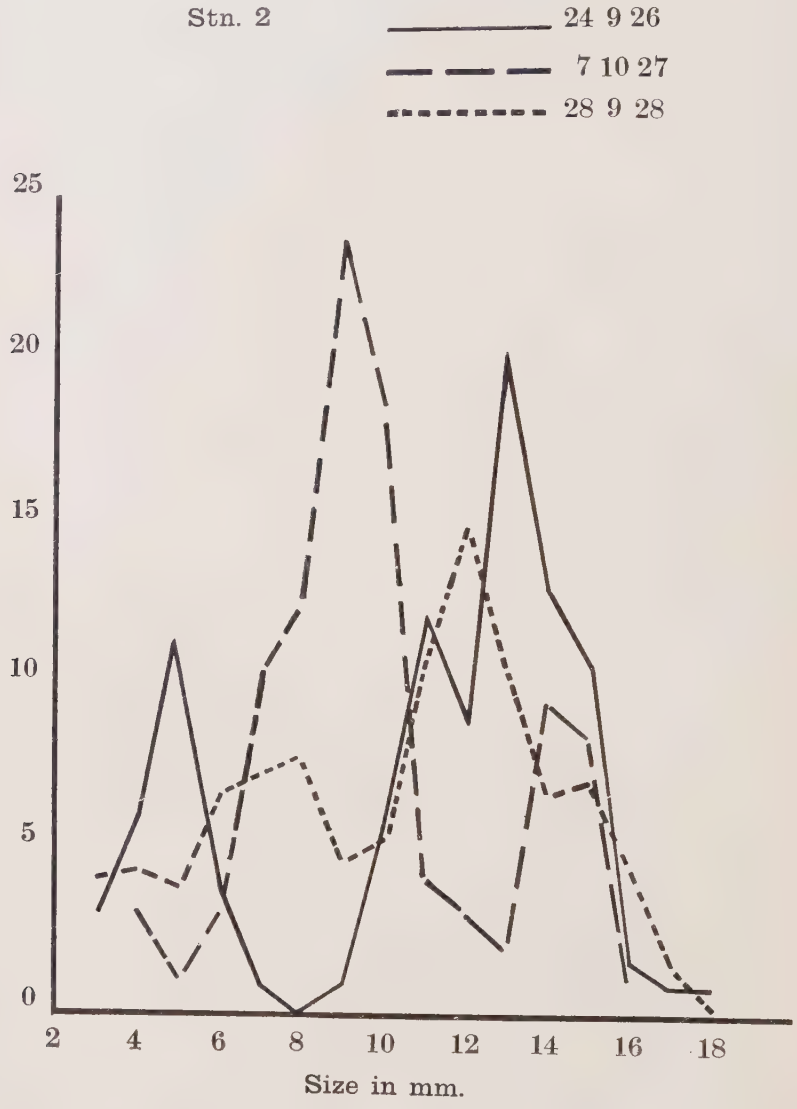

FIG. 4.—Graph showing the percentage (ordinate) of the catch at each mm. for Stn. 2 in Sept. 1926, Oct. 1927 and Sept. 1928.

On the size-frequency curve for March, 1928, there were modes at 9 mm. and 15 mm. By June that at 9 mm. had moved to 10 mm., but that at 15 mm. remained at the same figure. At the other end of the

curve the spat of 1927 was showing as a distinct group at 4 mm. By the end of September the mode at 4 mm. had moved to 8 mm., that at 10 mm. to 12 mm., while that at 15 mm. remained stationary.

Compared with 1927 growth was rather less, the modes for 1928 being about 1 mm. behind the corresponding ones for 1927.

In 1927 also the rate of growth from March to June was greater than that from June to the beginning of October, but in 1928 the position was reversed.

The results at this station again confirm the view of a missing year group on the curve for 1926, the rate of growth during 1928 having been of the same order as in 1927.

The 1926 spat was a prominent group at this station, as at Station 5. If we take the figures from 10 mm. to 15 mm. as representing it, the proportion of the population belonging to it was 52·5% and the actual numbers were 108 per "$\frac{1}{4}$ sq. m."

Stn. 6 (Table VI).

The collection made at this station in the end of September, 1928, was similar to those of the preceding years. The individuals were all very small and few exceeded 7 mm. in length.

There were no signs of any growth or of year groups as at Stations 2 and 5. There had been, however, a steady decrease from 325 in September, 1926, to 128 in September, 1928, per 20 cm. cube, as the following table shows.

Table I.

Table showing the decrease in the numbers of *Tellina tenuis* per 20 cm. cube at Station 6 from September, 1926, to September, 1928.

Date.	No. of *Tellina tenuis*
6.10.26	327
13.4.27	355
13.8.27	254
8.10.27	194
23.3.28	167
28.9.28	128

Stn. 7 (Table VI).

Again, as on previous occasions, the individuals at this station were only of very small size, the majority ranging from 3 mm. to 6 mm. As at Station 6, there had been practically no signs of growth during the whole year, but again there had been a very heavy mortality as the following table shows.

Table II.

Table showing the decrease in the numbers of *Tellina tenuis* per 20 cm. cube during 1928.

Date.	No. of *Tellina tenuis*.
8.10.27	143
23.3.28	66
28.9.28	18

The results from Stations 1 to 5, that is from that part of the range of the species from H.W.M. to L.W.M., are straightforward. The size-frequency curves show modes which move forward regularly and the course of events is orderly and logical.

At Stations 6 to 8, that is from that part of the range of the species below L.W.M., the results do not fit into the same scheme. When first examined in September, 1926, the specimens of *Tellina tenuis* were all fairly small (2, p. 701), and they appear to have remained at practically the same size ever since. Now elsewhere we find the species below L.W.M., although only in small numbers, but the size of the individual is often much greater than here. What, then, is the explanation of the state of affairs in Kames Bay? The most satisfactory explanation is that in the summer and autumn of 1926 huge numbers of spat settled on the ground from Stations 6 to 8, causing overcrowding to such an extent that the food supply has proved insufficient. Under such circumstances a species, after holding the ground for some time would, in the natural course of events, begin to die off, and this is exactly what has been taking place to a very marked extent during the present year (Tables I and II).

III. Rate of Growth of *Tellina tenuis* on the Hunterston Sands.

It was decided to make an exact comparison during 1928 between the rate of growth of *Tellina tenuis* in Kames Bay and in one of the other sands. A station near L.W.M. on the Hunterston Sands, Ayrshire Coast, was chosen and was examined at the same times as Kames Bay.

Hunterston Sands at Perch (Fig. 5. Table VII).

On the size-frequency curves there were in April two modes at 3 mm. and 9 mm. By June that at 3 mm. had moved to 5 mm. and that at 9 mm. to 10 mm. By the end of September the curve had greatly changed, for, as at Station 5, the group represented by the 10 mm. mode in June

had practically disappeared. Now this result was not due to insufficient sampling but represented the actual condition of affairs, for in view of such a marked change the matter could not be left undecided, and two repeat samplings were made, with exactly the same result.

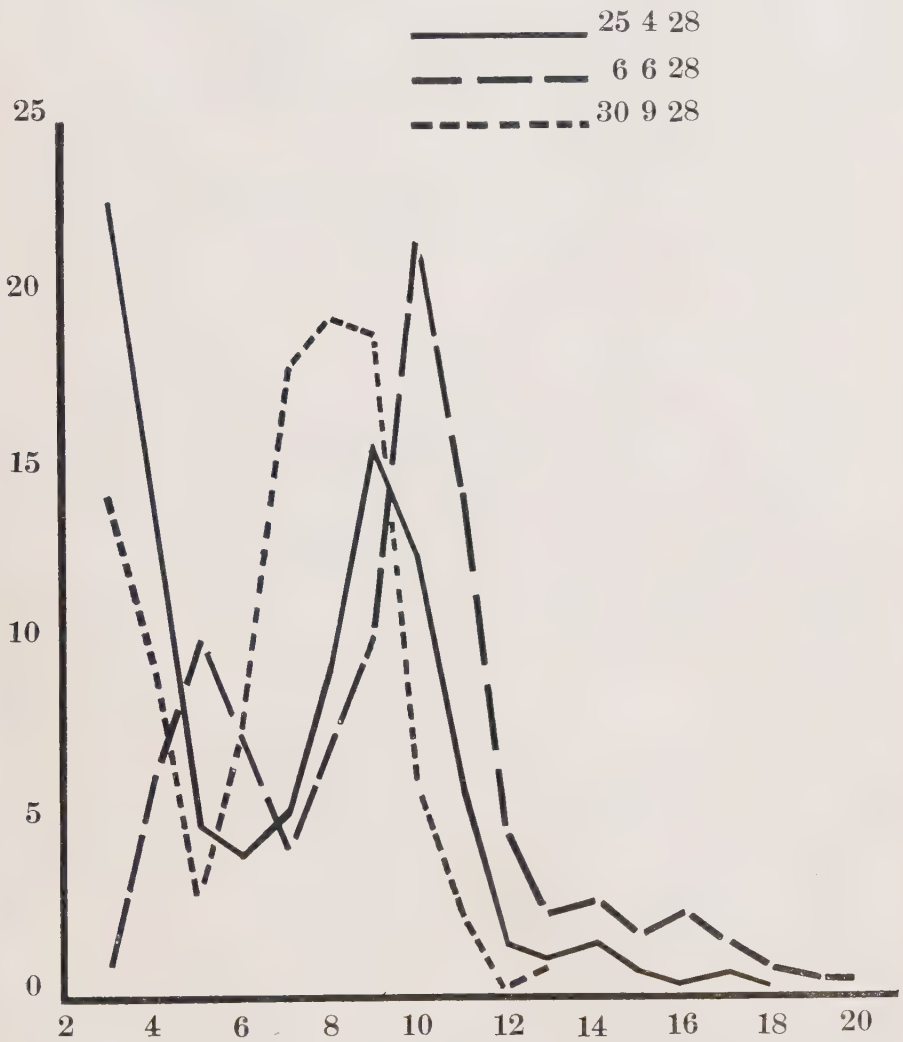

FIG. 5.—Graph showing the percentage (ordinate) of the catch at each mm. for the Hunterston Sands at L.W.M. in April, June and Sept. 1928.

To return to the curve, the mode at 5 mm. in June had moved to 8 mm. and the new spat had appeared at 3 mm. in September. The two modes on the September curve represent the 0+ group (1928 spat) at 3 mm.

and the 1+ group (1927 spat) at 8 mm. The 2+ group (1926 spat), which is still the dominant year group in Kames Bay and was, till June, here also, has gone. When picking over the samples the empty valves, whole and therefore not taken by fish, were found in large numbers, but what was the cause of the heavy mortality here, and to a lesser extent at Station 5 in Kames Bay, was not apparent.

If we take the April curve as roughly corresponding to the size-frequency distribution at the end of the previous autumn, growth, as in Kames Bay, has been rather less in 1928, the second mode being at 8 mm. as against 9 mm. last year.

The position of the mode at 8 mm. indicates that the rate of growth at this station is of the same order as that at Stations 2 or 3 in Kames Bay, and not as at Station 5, as the position on the beach would lead us to suppose.

IV. Distribution of Sizes passing the 2 mm. Sieve.

So far we have only dealt with the specimens retained by the 2 mm. sieve. In the earlier investigation the distribution and relative frequency of the sizes passing the 2 mm. sieve but retained by the 1 mm. sieve were also dealt with, and for comparison a similar set of observations was made at Stations 2, 5, 6, and 7 in 1928. Compared with 1927 there has been a marked reduction in the numbers at all stations by the end of 1928, as the following table shows.

Table III.

Table showing the numbers of *Tellina tenuis* passing the 2 mm. sieve but retained by the 1 mm. sieve in Kames Bay.

	Contained in a 20-cm. cube.		Contained in a $\frac{1}{4}$ sq. metre.	
	Stn. 7.	Stn. 6.	Stn. 5.	Stn. 2.
Sept. 1927	167	85	102	20
Sept. 1928	0	3	60	0

V. Amount of Spat in Various Years.

There is good evidence that the spat which settled on the bottom and survived until the autumn varied during the years 1926–8. The year 1926 stands out as one of unusual abundance. If we consider the individuals of 3 mm. and 4 mm. in the end of September as representing the spat, the numbers per $\frac{1}{4}$ sq. m. at Stations 2 and 5 for each year were as follows.

Table IV.

Table showing the numbers of specimens 3 mm. and 4 mm. in length at Stations 5 and 2 in September of each year per $\frac{1}{4}$ sq. m.

	Stn. 5.	Stn. 2.
1926 . .	655	12
1927 . .	272	13
1928 . .	213	26

So far as the collections made by the 2 mm. sieve are concerned 1927 and 1928 seem to be about equal, but when the figures in Table III are taken into consideration 1928 appears the poorer.

VI. History of the 1926 Spat.

It has already been pointed out how the 1926 spat has survived as a dominant group, and it is possible to trace its history since 1926.

The group was found as spat in September, 1926, and was present in large numbers from Station 7 to half-tide, and in small numbers to H.W.M.

In September, 1928, below L.W.M. it still remained on the ground, but showed little growth, and had steadily declined in numbers. At Station 7 a few remained and the numbers had fallen to a third at Station 6.

At, and above, L.W.M. the modes remained at a standstill during the winter months, but showed progress during the summer months, the shift of the mode being least at Station 5 and proportionately greater at each station nearer H.W.M. The halts and progress of the modes are clearly seen in Table V.

Table V.

Table showing the position of the modes of the 1926 spat, from September, 1926, to September, 1928, for each time of collecting, for Stations 2 and 5.

Date.	Stn. 5.	*Yearly increment.*	Stn. 2.	*Yearly increment.*
24.9.26 . .	3 mm.			
13.4.27 . .	3 ,,		3 mm.	
20.6.27 . .	5 ,,	4 mm.	6 ,,	6 mm.
13.8.27 . .	6 ,,		8·5 ,,	
7.10.27 . .	7 ,,		9 ,,	
23.3.28 . .	7 ,,		9 ,,	
7.6.28 . .	8 ,,	2 mm.	10 ,,	3 mm.
28.9.28 . .	9 ,,		12 ,,	

In 1927 the mode shifted from 3 mm. to 7 mm. at Station 5 and from 3 mm to 9 mm. at Station 2. During 1928 the shift at Station 5 was from 7 mm. to 9 mm., and at Station 2 from 9 mm. to 12 mm. In other words, the movement during 1928 was exactly half of that during 1927 at both stations. This result is in accord with that which Orton (1) has found for *Cardium edule*. In that species, for four years, each annual increment was approximately half of the preceding year.

If, in the case of the Lamellibranchs, it can be assumed that the annual increment is even approximately half that of the preceding year, an important point is established, which may give a means of estimating the age of the numerous small, but from the economic point of view important, species. In these species it might be possible to measure the first full year's increment, but it would probably be very difficult to follow subsequent growth.

Table VI.

Stn. 2.

Percentages of catch at each mm. length.

mm.	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Total specimens.
23.3.28	0·7	1·6	3·7	4·7	8·0	13·1	17·5	14·8	5·0	3·8	6·7	7·4	7·9	4·6	0·5	0·2	674
5.6.28	5·1	9·8	7·2	4·4	5·1	4·7	9·0	13·9	10·4	4·8	4·1	7·7	8·4	3·9	0·9	0·2	662
28.9.28	4·1	4·4	3·8	6·7	7·3	7·7	4·7	5·3	10·7	14·9	10·5	6·6	7·3	4·5	1·4	0·2	684

Stn. 5

Percentages of catch at each mm. length.

mm.	3	4	5	6	7	8	9	10	11	12	13	14	15	Total specimens.
23.3.28	14·8	8·9	8·9	13·1	15·1	10·0	4·8	7·1	8·0	6·7	2·3	0·4	0·1	2002
7.6.28	13·6	10·9	5·6	5·3	10·7	13·9	12·2	7·7	5·1	8·7	5·3	1·2	0·2	1351
28.9 28	20·6	7·5	6·7	10·4	6·8	9·4	13·1	10·5	7·0	4·9	2·5	0·3	0·2	1519

Stn. 6.

Percentages of catch at each mm. length.

mm.	3	4	5	6	7	8	9	10	11	12	Total specimens.
29.9.28	20·9	22·1	20·9	14·6	13·2	5·0	1·9	0·6	0·0	0·6	158

Stn. 7.

Percentages of catch at each mm. length.

mm.	3	4	5	6	7	Total specimens.
29.9.28	32·3	22·6	29·0	12·9	3·2	31

Table VII.

Hunterston Sands (at Perch).

Percentages of catch at each mm. length.

mm.	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Total specimens.
25.4.28	22·7	13·9	4·9	4·1	5·3	9·3	15·8	12·7	5·9	1·3	1·0	1·2	0·7	0·3	0·7	0·2	–	–	589
6.6.28	0·9	6·3	10·1	7·5	4·2	7·3	10·1	21·8	14·5	4·9	2·3	2·6	2·1	2·3	1·4	0·7	0·5	0·5	427
30.9.28	14·3	9·5	2·8	7·7	18·0	19·3	18·8	6·0	2·2	0·4	1·0	–	–	–	–	–	–	–	496

VII. SUMMARY.

1. The present paper is a direct continuation of the work done at Millport during 1926 and 1927.

2. As before, *Tellina tenuis* showed no growth during the winter months.

3. As before, the rate of growth at L.W.M. was less than that near H.W.M.

4. Below L.W.M. there seemed to have been no growth during the year, but there had been a heavy mortality during 1928.

5. Above L.W.M. the rate of growth during 1928 was of the same order as that of 1927, and the view that a year group was unrepresented on the 1926 curve seems justified.

6. At the end of September, 1928, the 1926 spat still formed a large and well-marked group.

7. The history of the 1926 spat is traced, and the annual increment found to be halved in succeeding years.

VIII. LITERATURE CITED.

1. Orton, J. H. Rate of Growth of *Cardium edule*. Jour. Mar. Biol. Assoc. New Series, Vol. XIV, No. 2, 1926.

2. Stephen, A. C. Notes on the Biology of *Tellina tenuis*. Jour. Mar. Biol. Assoc. Vol. XV, No. 2, April, 1928.

On Methods of Reproduction as Specific Characters.

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With 11 Figures in the Text.

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INTRODUCTION.

The primary aim of this paper is to show that among certain Actinians investigated, the species are sharply differentiated by their divers methods of reproduction; and to point out that the general question of species is one which is worthy of the attention of experimental biologists. Arguments supporting these contentions will be found in Section 7.

I should like to make the following acknowledgments. I have received a grant, which has made the work described possible, from the Department of Scientific and Industrial Research. I have received interest and advice from Prof. Watson, and invaluable assistance (detailed below) from Mr. W. Edgar Evans. The whole cultural side of the work was carried out by my wife, who also provided Text-Figs. 2 and 3, and the sections from which they were drawn. I am very much indebted also to the Plymouth staff and to Miss M. Delap, of Valencia, and Mr. Elmhirst, of Millport, for the collection of the large amount of material required.

1. THE METHODS OF REPRODUCTION PREVALENT AMONG ACTINIANS.

The sea-anemones which have been specially studied for this part of the paper are the following :—

1. *Sagartia lacerata* (Dalyell).
   [*S. coccinea* of Gosse, but not *Actinia coccinea* Müller].
2. *S. elegans* (Dalyell).
   [Various colour-varieties were used].
3. *S. anguicoma* (Price).
   [More usually known in this country as *S. viduata* (Müller). It is not, however, identical with the latter, which is non-British.]
4. *S. troglodytes* (Price).
   [Both varieties of this species were used, the typical form (var. *decorata* Stephenson) and the var. *ornata* (Holdsworth)].
5. *S. sphyrodeta* Gosse.
6. *Cereus pedunculatus* (Pennant).
   [Commonly known as *Sagartia bellis* (Ellis)].
7. *Diadumene cincta* Stephenson.
8. *D. luciæ* (Verrill).
   [Also known as *Sagartia luciæ* Verrill].

In the above-mentioned species the following methods of reproduction occur.

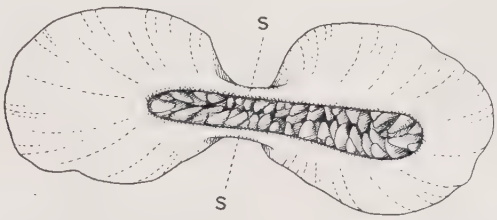
1. *Oviposition, etc.*

The deposition of either sperms, ova, or both, has been observed in several of the species under consideration; but data relating to this are scanty, and are insufficient to permit us to form any adequate idea as to the extent to which the various species deposit ova in the wild state. Further information is badly needed about the breeding-seasons of anemones and about the life-history of their gonads. From the point of view of this paper, however, it may be taken as probable that all or most of the species concerned deposit ova on occasion. The oviparous habit therefore, being general, is not considered in detail here. It could only be of interest to the issue involved if it could be shown that the viviparous species never deposit ova. This, however, is not the case. In *Sagartia troglodytes* the animal is hermaphrodite, and has been seen to discharge ova and spermatozoa simultaneously, or one a short time after the other; and this probably occurs in nature as well

as under aquarium conditions, although the species is habitually viviparous. In the other viviparous form, *Cereus pedunculatus*, the animal is also hermaphrodite, and here I am not aware of cases in which it has been seen to deposit ova. Specimens undergoing irritation have been known to discharge early embryos (observed by Signor Jucci at the Plymouth Laboratory), but this is not, as far as I know, a normal occurrence.

2. *Viviparity* (*Sagartia troglodytes* and *Cereus pedunculatus*).

In the viviparous forms, which are sometimes (perhaps always) hermaphrodite, fertilisation is internal, and the embryos develop in the cœlenteron of the parent, achieve their metamorphosis, and are



Text-Fig. 1.—*Sagartia sphyrodeta*. A specimen in the act of dividing into halves. The base, column-wall, and throat have actually ruptured, and the two parts are held together by the sphincter (S) and by part of the oral disc (not visible in the sketch). Enlarged more than 5 diameters.

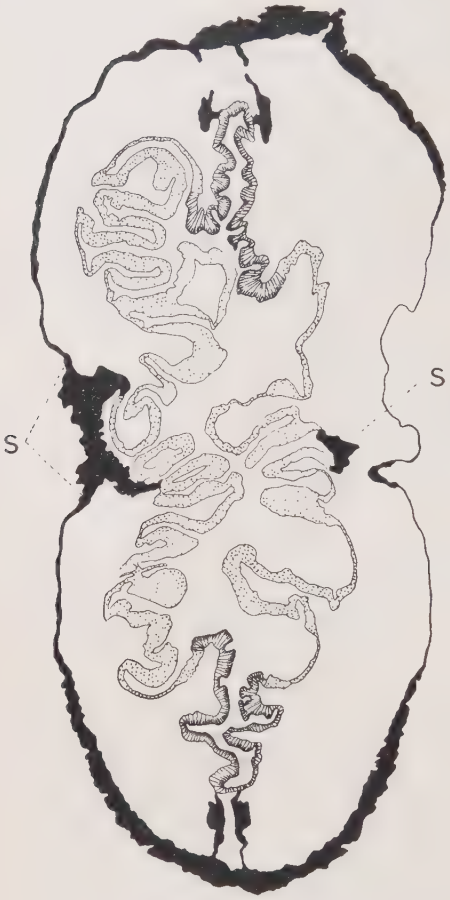
fully-formed small anemones by the time they escape from the parent. This does not necessarily apply to all the ova of any given specimen; and although fertilisation in the case of the young which are retained is certainly internal, it does not follow that it is effected by spermatozoa belonging to the individual which produced the ova. An anemone with some of its viviparous young* is illustrated in Text-Fig. 5.

3. *Longitudinal Fission* (*Sagartia sphyrodeta* and *Diadumene luciæ*).

In this method the animal elongates in one direction, the two halves of the base moving away from each other. Rupture results, and each of the halves heals up and forms a new individual. The halves may be equal or unequal in size, but each normally possesses tentacles, so that a complete new set does not have to be regenerated by either half. The fission tears the base and the column-wall, and also involves the throat, in many cases if not always. These statements do not apply to all cases of fission among Actinians, since there are apparently instances in which

* For the sake of brevity the term viviparous young has been used throughout to denote viviparously produced young.

a gradual separation of parts takes place ; but they apply to the normal fissions in the species here dealt with, where the process is one of rupture, and is of relatively brief duration, often lasting for a matter of hours only. In some cases more than two pieces arise from a fission.



Text-Fig. 2.—*Sagartia sphyrodeta*. A transverse section of the specimen shown in Text-Fig. 1, after fixation. See text. Column-wall and directive mesenteries black ; tentacles and oral disc stippled ; throat shaded with strokes. S, sphincter, cut through in two places. All mesenteries are omitted save the directives.

In the interesting and instructive paper recently published by Matthai (1926), on colony-formation in Astræid corals, this author concludes from his studies, with full justification, that true fission, involving division of the throat, does not occur among the Astræidæ, and that there is no evidence of it among the Madreporaria.* This being so, it may be relevant to emphasize the fact that it *does* occur among the Actiniaria. I have personally witnessed a number of instances of its occurrence in anemones (and many other examples of the allied process of laceration), and in one case I was fortunate in catching a specimen of *Sagartia sphyrodeta* at a stage in the process at which the base and throat had been torn completely in two, but only part of the body-wall had given way. The two halves were still connected by the sphincter and by part of the oral disc. A sketch of this specimen, from the living animal, is shown in Text-Fig. 1. It was fixed immediately after it had been sketched and was subsequently sectioned. Two sections from the series are illustrated in Text-Figs. 2 and 3. In the section shown in Fig. 2 the body-wall and oral disc of the two

* In this connection it should be remembered that in Corynactis fission certainly does occur, and may involve the mouth (an observation confirmed by Evans, who has seen fission many times in *C. viridis*). I have tried to show elsewhese (1921, p. 510) that Corynactis is probably an aberrant Madrepore which secretes no skeleton, and not an anemone. But this does not affect the question of the typical Madreporaria.

sides are continuous, and part of the throat is seen in each half. In the other section, Fig. 3 (cut at a lower level than the first), the base, the body-wall, and throat of each half have been torn away completely from the other half.

That fission should occur frequently among the Actiniaria and not among the skeleton-building Madreporaria serves only to emphasize the essential difference in tendency between these groups. In the Actiniaria we are dealing with non-colonial organisms which are typically muscular creeping-forms (no other group of the Cœlenterates offers a parallel to this creeping habit of the Actinians), secreting no skeleton, and inclined to divide by means of fission or laceration. In the Madreporaria, on the other hand, it is a question of animals which are frequently colonial, entirely sedentary, nearly always building a skeleton, and reproducing asexually by means of budding of one kind or another, and not by fission; budding is not characteristic of Actiniaria, although cases of it are on record.

In *Gonactinia prolifera* and *Aiptasia couchii, transverse fission* takes place; but this is a process of rare occurrence among anemones and not found in the species studied here. In *Gonactinia* the process is one resembling in some respects the strobilisation of a scyphistoma.

Text-Fig. 3.—A section from the same series as that from which was taken the section shown in Text-Fig. 2; this one is cut at a lower level. See explanation beneath Text-Fig. 2, and also the text. B, base—the animal was somewhat curled up after fixation, so that in the lower part base and column-wall come into the same section on either side.

Lastly it may be noted that in almost any collection of specimens of *Sagartia sphyrodeta* or *Diadumene luciæ* freshly brought in, it is possible to detect a certain proportion of

individuals which show unmistakable signs of having recently undergone fission. This is revealed by the presence of a sector of regenerating tissue, of different colour from the rest. A sketch of an expanded specimen which had recently divided is shown in Text-Fig. 4.

4. *Laceration by Tearing* (*Sagartia elegans* and *Diadumene cincta*).

In this method no division of the animal occurs so long as it remains stationary (except in the event of its putting out a basal extension and afterwards withdrawing this in such a way that a rupture occurs), but if it begins to creep away there may be left behind a larger or smaller

Text-Fig. 4.—Outline of a specimen derived from a recent fission. The shape of the disc (the edge of which is indicated by a dotted line) is modified. The regenerating region (approximately) is stippled. The primary tentacles are marked I. Enlarged about 10 diameters.

fragment, attached to the substratum. The separation of the piece is an actual tear involving a stretching of the region of rupture ; it may take place on a perfectly smooth surface, or it may occur when the animal climbs over a rough place or an edge ; in animals kept in finger-bowls a laceration is often produced if the anemone climbs over the edge of the bowl. In my experience the piece torn off is never large enough to contain any portion of the disc and tentacles of the parent, although it includes part of the base, the body-wall, and the lower ends of mesenteries, and may be more than a centimetre in diameter. In *Diadumene cincta* the animal, after having produced a laceration which has become almost separated from it, occasionally tries to recall the laceration and heal it up again. In the cases observed this resulted in death.

An example in which six lacerations had separated from a single specimen of *Sagartia elegans* is illustrated in Text-Fig. 6.

5. *Laceration by Constriction* (*Sagartia lacerata*).

Here the parent anemone usually (though not necessarily) remains stationary, and from the expanded edge of its base small capes and islands become constricted off (Text-Fig. 8). These may remain quite close to the parent, or may move away to some distance from it, often remaining connected with it for a time by a thin stolon before complete separation takes place. Here, as in laceration by tearing, the fragments contain base, body-wall, and mesenteries only; and they are usually small, a few millimetres only in diameter, whereas by the other method rather large pieces are sometimes torn off. A specimen from which a number of lacerations had separated is illustrated in Text-Fig. 7.

2. DATA RELATING TO THE SUBJECT COLLECTED BY W. E. EVANS.

For some years Mr. W. Edgar Evans, B.Sc., of the Royal Botanic Garden at Edinburgh, has maintained in his house a private marine aquarium of an unusual type. The whole construction and mode of maintenance of his aquarium are excellent, and during the period when Mr. Evans was able to give a considerable amount of attention to it, the health of the animals contained in it was of an extremely high order, such as I have seen equalled nowhere else. For some time now, the tanks have been used almost exclusively for sea-anemones, and all the available British species have been under observation in them at one time or another. Details of the construction and method of maintenance of this aquarium will be found in *Discovery*, Vol. VII, No. 74, 1926, p. 51.

The methods of reproduction detailed in the last section have been known to naturalists for many years, but the general idea connected with them seems to have been that they are of somewhat erratic occurrence among Actinian species, and that one anemone is as likely to undergo fission, for instance, as another. Although it has been quite clearly understood by certain workers (see p. 154) that some of the methods are characteristic of given species, no special study has been devoted, so far as I am aware, to reproductive methods considered purely as specific characters. While observing the anemones in his collection over a period of several years, Mr. Evans noticed that no one species (save *Aiptasia couchii*) ever employed more than a single method of reproduction (apart from the deposition of sperms and ova), and some of his notes are given below. The value of his observations lies partly in

the fact that his aquarium has been one of quite exceptional efficiency, and partly in that, though his records cover but few specimens, many of these were under continuous observation for several years.

The details are as follows. The calculation of times is up to June 27th, 1926. In the majority of cases a separate account of each specimen was kept in an aquarium notebook.

Sagartia troglodytes.

The records available cover 22 specimens, and 21 were still alive on the date to which the calculations run. Of these, three had been under observation for between 4 and 5 years (two for nearly 5), five for between 3 and 4 years, three for between 2 and 3 years, and the rest for less than a year.

During this time, reproduction by fission or laceration was never seen or even suspected, whilst the production of viviparous young was so normal and frequent in well-fed specimens that it was not as a rule entered in the aquarium notebook, although recorded on certain occasions. Damage to specimens while collecting in the wild usually resulted in the escape of viviparous young. A sample of the entries in the notebook is as follows :—

Colour-Variety.	Obtained.	Died.	Locality.	Remarks.
ornata	7.9.25	Living	Valencia, Co. Kerry	Viviparous young at intervals.
scolopacina	29.5.22	31.5.24	Longniddry, Forth	Viviparous young produced
ornata	1.4.23	Living	Torquay	Viviparous young occasionally.
lilacina	8.10.22	Living	Joppa, Forth	No reproduction observed.

Sagartia elegans.

The records available cover 14 specimens, and 7 were still alive on the date to which the calculations run. Of these, two were under observation for between 3 and 4 years, five for between 2 and 3 years, four for between 1 and 2 years, and the rest for less than a year. In this species reproduction by laceration was found to be so constant a characteristic of well-fed specimens that again only a certain number of instances were actually entered in the notebook. No healthy specimen was ever kept which did not undergo laceration. Neither fission nor the production of viviparous young was ever observed. A sample of the entries in the notebook is as follows :—

Colour-Variety.	Obtained.	Died.	Locality.	Remarks.
ornata*	2.11.23	12.5.25	Millport, Clyde	Laceration often. Over 10 pieces before 14.12.24.
venusta	20.1.25	Living	Valencia, Co. Kerry	Laceration occasionally.
venusta	20.9.22	8.25	Tenby	Laceration began 23.12.22, next occurred 9.1.23, later often.
nivea	20.9.22	Living	Tenby	Laceration frequently.

Sagartia anguicoma.

The records available cover 6 specimens, and 5 were still alive on the date to which the calculations run. Of these, one was under observation for between 4 and 5 years, one for between 3 and 4 years, the others for less than a year. During this period fission and laceration were never seen or even suspected; production of viviparous young was suspected (not seen) on one occasion, but subsequently definitely disproved.

Beyond the above data general notes are available to the effect that in *Cereus pedunculatus* viviparous young were produced at all seasons; that in *Sagartia sphyrodeta* fission was observed at various times, e.g. 10.12.22. and 29.3.25; that in *S. lacerata* laceration occurred at all seasons; that in *Diadumene luciæ* fission occurred at all seasons if the animals were well fed; and that at *D. cincta* laceration at all seasons was observed.

Further observations by Mr. Evans, on species not specially dealt with in this paper, are given below in Section 6. For the moment, however, it is enough to say that the results above recorded fit in exactly with those derived from the experiments detailed in the next section.

3. ACCOUNT OF EXPERIMENTS AT PLYMOUTH.

I was at first unwilling to agree with the conclusions reached by Evans as a result of his aquarium observations; but subsequently I became much interested in the subject, and decided to undertake some experiments, in the hope of putting the matter upon a more satisfactory basis. I was able to carry out these experiments during five months' residence at Plymouth, January to June, 1927. I regret that I was unable to carry them on for a longer period, because the reproductive processes are slow, and a run of two or three years would have been much better than a few months. Again, the total number of experimental animals (over 400) was not as large as I should have wished, but

* *Sagartia elegans* and *S. troglodytes* both possess a variety named "*ornata*."

since many of these had to be accommodated each in a separate finger-bowl, the question of accommodation and maintenance became serious. The time required for keeping clean and feeding individually as many specimens as this is considerable.

The method of experiment was as follows. In the first place it was desired to isolate a number of individuals of each of the species (see p. 148) chosen for experiment, so that a detailed record could be kept of the

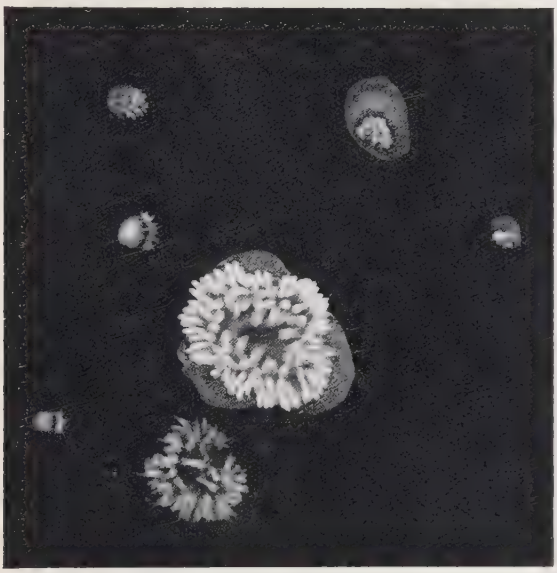
Text-Fig. 5.—From a photograph of a specimen of *Bunodactis verrucosa*, with a number of viviparous young which it had recently produced. The parent is in a partially contracted condition. Slightly reduced.

activities of each animal. This was done by placing each individual in a separate finger-bowl, and awaiting results. The conditions were kept as uniform as possible for all the species, and the finger-bowls were cleaned and their occupants fed at regular intervals. Great care was taken to provide as adequate aeration as possible, and to keep the animals healthy. The whole of them were inspected daily and notes made of anything which occurred. The general mortality was so low as to be negligible except in two difficult species (*S. sphyrodeta* and *D. luciæ*) which could not be maintained as satisfactorily as the others with the facilities available. It was necessary to use ordinary tank-water, and this is not

of the very best quality for delicate species, which also require special conditions in other respects.

In the case of many of the finger-bowls, it was found sufficient to stand them on the slate slabs underneath some of the tanks, and to aerate them for a certain period, daily, by means of a special apparatus which changed the water at the same time.

Other finger-bowls were kept in running water in a tank, the water-level being kept below the tops of the finger-bowls so that their isolation



Text-Fig. 6.—From a photograph of a specimen of *Sagartia elegans*, with six smaller specimens round it. The latter were all produced as lacerations torn away from the parent when it moved from one place to another; all of them have regenerated. Slightly reduced.

was maintained; these were aerated by flooding them once a day. A further number of bowls was kept under water which was in circulation; these were not, therefore, fully isolated from one another (e.g. spermatozoa could escape from one bowl to another), but from the point of view of laceration, fission, and viviparous young, the isolation was adequate.

For a considerable part of the period of experiment, about half the specimens of several species were kept in special finger-bowls which had been entirely lined with a mixture of Portland cement and gravel, sometimes with stones and shells fixed in it. This was in order to provide a rough surface for the animals, with the idea that lacerations might be

produced more freely on this than on glass. It also gave an excellent opportunity to species which do not normally lacerate, to do so—and thus acted as an additional control. It was found, however, that the kinds which do not lacerate showed not the least tendency to do so on the rough surface; these creatures will glide over edges which would often provide an irresistible opportunity for lacerating, in the other species, without doing so. Moreover, the lacerating species seemed little, if at all,

Text-Fig. 7.—From a photograph of a specimen of *Sagartia lacerata*, also showing a number of small individuals, all produced as lacerations (by the constrictional method) from the one parent. Both the parent and such of the young as possessed them had withdrawn their tentacles, as is usual in this species when exposed to daylight. Slightly reduced.

more inclined to tear themselves on the rough surface than on the smooth. These cement bowls are useful for various purposes, but have to be soaked first in fresh and later in sea-water, and scrubbed free from the crystals which form on the cement, for some time before they are fit for use. In the detailed records of the experiments no distinction is made between cases in which the animals were in glass bowls for the whole period, and those in which they were at first in glass bowls and later in cement ones; because it was found that the change had no effect on

the essential conditions of the experiment. Most of the cement bowls were kept under circulation.

In the second place it was desired to ascertain whether, in species which do not reproduce by any asexual method under natural conditions, portions cut off artificially would regenerate as readily as in the case of species which lacerate of their own accord. For this purpose four species were chosen, two belonging to each category. Prior to each operation, a healthy adult anemone was allowed to settle comfortably in a finger

Text-Fig. 8.—A specimen of *Sagartia lacerata* which had attached itself to glass; viewed through the glass from below the base. Several pieces are becoming or have become separated from the edge of the base, and in four of these tentacles are visible. Slightly enlarged.

bowl, or on a glass slide; when it had become firmly attached, small portions were separated from the edge of its base by tangential cuts with a small, sharp, sterilised scalpel. After the cuts had been made the parent anemone was removed and the glass cleaned, this leaving behind the separated pieces attached to the bowl. The bowls containing the pieces were kept under circulation in a tank, and the pieces allowed to regenerate. Plymouth tank-water is not an ideal medium for such experiments, because it contains a soft sediment which settles continually in the bowls and on the regenerating pieces, so that it is not easy to keep them sufficiently clean; if the sediment is allowed to

accumulate for too long the pieces die. Nevertheless, the general results were satisfactory. The details are as follows :—

A. Experiments on the Natural Methods of Reproduction.*

I. *Sagartia elegans.*

Experiment 1.

32 specimens were used (30 to begin with, the other two to replace specimens which died). The duration of the experiment was 21 weeks and 5 days (January 13th to June 14th), and during that period 52 lacerations were produced, all by the tearing method. The number of specimens which underwent laceration was 21 (65·6% of the whole number).

Experiment 2.

26 specimens were used (25 to begin with, the other one to replace a specimen which died). The duration of the experiment was 14 weeks and 2 days (March 6th to June 14th), and during that period 8 lacerations were produced, all by the tearing method. The number of specimens which underwent laceration was 5 (19·2% of the whole number).

Other data.

From about 30 specimens which were not included in the main experiments, but were kept in other vessels, 20 lacerations were produced during the period of the main experiments.

Summary.

From over 80 specimens of *S. elegans* there were produced 80 lacerations during the course of the experiments; by no means every specimen produced a laceration during this period, but some specimens produced more than one, so that the total number produced averages about one laceration to each individual used.

II. *Sagartia lacerata.*

Experiment 1.

15 specimens were used. The duration of the experiment was 20 weeks and 5 days (January 15th to June 9th), and during that period 172 lacerations were produced, all by the constrictional method. All the specimens underwent laceration, the respective number of lacerations produced by the different individuals being as follows: 1, 6, 11, 8, 13, 15, 9, 28, 8, 13, 40, 1, 8, 1, 7.

* In this account of the experiments it is to be understood that no method of reproduction occurred in any experiment except the one recorded.

Experiment 2.

21 specimens were used. In this case all were contained in a single bowl, and the lacerations were removed as formed. Between February 11th and June 14th (17 weeks and 4 days), 116 lacerations were produced. One adult was removed on April 19th.

Summary.

From 36 specimens of *S. lacerata* there were produced 288 lacerations in the course of the experiments.

III. *Sagartia sphyrodeta.*

Experiment 1.

27 specimens were used (21 to begin with, 6 to replace specimens which died). Other specimens died before the end of the experiment, and were not replaced—total deaths 12. The duration of the experiment was 21 weeks (January 12th to June 8th), and during that time 7 specimens underwent longitudinal fission, two of these being further subdivisions of the halves resulting from a previous fission.

Experiment 2.

11 specimens were used (7 to begin with, 2 to replace specimens which died, and 2 added later). Other specimens died before the end of the experiment, and were not replaced—total deaths 5. The duration of the experiment was 16 weeks and 1 day (February 15th to June 8th), and during that period no fission occurred.

Other data.

Two specimens not included in the above experiments were observed to undergo longitudinal fission, and from among other specimens collected 9 showed unmistakable evidence of having recently undergone fission, the regeneration-zone being clearly marked.

Summary.

Among the 38 experimental specimens 7 cases of fission occurred during the period of observation; two other cases were observed in specimens outside the experiments. Nine further specimens collected had recently undergone fission.

IV. *Sagartia troglodytes* var. *decorata.*

Experiment 1.

16 specimens were used (15 to begin with, one to replace a specimen which escaped). The duration of the experiment was 20 weeks and 6 days (January 19th to June 14th), and during that period none of the

specimens underwent any form of asexual reproduction, nor did any of them produce viviparous young. The gonads appeared to be ripening towards the end of the experiment, so that the time for the production of viviparous young in these specimens would be later in the year. This is the only negative result reached which should have been positive; for there is ample evidence from other quarters to show that this form is viviparous.

V. *Sagartia troglodytes* var. *ornata*.

Experiment 1.

15 specimens were used. The duration of the experiment was 21 weeks and 3 days (January 15th to June 14th), and during that period 20 viviparous young were produced. These were produced by 6 of the specimens, the rest (60% of the whole number) producing nothing.

Experiment 2.

In this case 48 specimens were divided out among three vessels. Between February 2nd and April 9th (9 weeks and 3 days) they produced among them 56 viviparous young.

Other data.

7 viviparous young were produced by specimens received from Millport on April 24th—produced on April 25th.

Summary.

63 specimens produced among them 76 viviparous young during the period of observation. Seven other viviparous young were produced by further specimens (number unknown) of the species, on April 25th. The period of the experiments did not cover the prolific season of production.

VI. *Sagartia anguicoma* ("*viduata*").

Experiment 1.

15 specimens were used. The duration of the experiment was 21 weeks and 3 days (January 15th to June 14th), during which time no asexual reproduction of any kind occurred, nor were any viviparous young produced.

VII. *Cereus pedunculatus* (*Sagartia bellis*).

Experiment 1.

15 specimens were used. The duration of the experiment was 21 weeks and 3 days (January 15th to June 14th), during which time 110 viviparous young were produced. These young were produced by 11 of the

parents, the other four producing none. The numbers produced by the 11 adults in question were respectively 19, 2, 11, 16, 6, 37, 3, 5, 1, 3, and 7.

Experiment 2.

In this case 24 specimens were kept together in a tank, and the young removed as born. Between March 26th and June 16th (11 weeks and 5 days), 104 viviparous young were produced.

Other data.

One specimen not in either of the above experiments produced 12 viviparous young between April 19th and June 14th.

Summary.

40 specimens produced among them 226 young during the period of observation.

VIII. *Diadumene cincta.*

Experiment 1.

16 specimens were used (15 to begin with and one to replace a specimen which died). These were at first placed each in a separate finger-bowl, as usual, but later on some of them were transferred to a single square dish containing stones and gravel, so that they could be given a type of aeration which suited them better. The duration of the experiment was 21 weeks and 4 days (January 14th to June 14th), and during that time 8 lacerations were produced, all by the tearing method. In two cases the animal tried to recall the laceration before it had quite separated off; this resulted in death.

Other data.

A specimen outside the above experiment produced a laceration by the tearing method on March 22nd.

IX. *Diadumene* ("*Sagartia*") *luciæ.*

Experiment 1.

We were unable to obtain good material for this experiment. The few specimens available were all very small, and not in first-rate condition. This accounts for the poor result. Moreover, such small specimens (a few millimetres only in diameter) are difficult to keep, under the conditions of the experiment, and although 22 specimens in all were used (15 to begin with, the others to replace those which died), only 3 were still alive after May 22nd. The experiment started January 12th–20th. During the experiment 5 specimens underwent longitudinal fission.

Other data.

A specimen collected on April 19th had recently undergone fission.

The net result of the above experiments and observations is summarised in the following table, which shows the total number of new animals produced by any method in each of the species used, within the period of observation (about 21 weeks). In the cases of *S. sphyrodeta* and *D. luciæ* the collected specimens which had recently undergone fission are included. The result is discussed on page 159.

Species.	Fission.	Laceration by Tearing.	Laceration by Constriction.	Viviparous Young.
Sagartia elegans	—	80	—	—
S. lacerata	—	—	288	—
S. sphyrodeta	18	—	—	—
S. troglodytes var. decorata	—	—	—	—
S. troglodytes var. ornata	—	—	—	83
S. anguicoma	—	—	—	—
Cereus pedunculatus	—	—	—	226
Diadumene cincta	—	9	—	—
D. luciæ	6	—	—	—

B. Experiments in Artificial Laceration.

The results of these experiments are summarised in the table on the opposite page.

The pieces were not all cut off on the same date, because it was impossible to obtain enough material in suitable condition for operation, at any single time early in the period of experimentation. The experiments therefore lasted longer for some pieces than for others, the minimum time being 6 weeks and 5 days; but it must be remembered that the experiment for any given piece may be regarded as being over when that piece has attained full development, so that in this sense some of the experiments were complete long before the end of the whole period of experimentation. The variation in date of starting makes no essential difference to the result, because the highest mortality normally occurs shortly after the operation, and it may be taken that if an amputation survived for the minimum period mentioned it would, in the ordinary course of events, ultimately become fully developed even if it had not already done so by the end of the experimental period.

Species.	Number of specimens used.	Number of pieces cut off.	Number which survived until end of experiment.	Time taken to regenerate tentacles.			Time taken to acquire mouth and disc as well as tentacles.		
				Minimum.	Maximum.	Average.	Minimum.	Maximum.	Average.
Sagartia elegans	23	60	55 (91·7%)	2 weeks 1 day	9 weeks 1 day	4 weeks 6 days 54	4 weeks 5 days	14 weeks 6 days	8 weeks 5 days 36
Sagartia troglodytes var. decorata	21	76	22 (28·9%) 32 made some attempt at regeneration, but 2 only became fully developed	5 only achieved tentacles: 5 weeks 3 days	8 weeks 4 days	7 weeks 3 days 4	2 only achieved mouths, they were perfect after 12 weeks 4 days.		
Sagartia anguicoma	18	67	39 (58·2%)	3 weeks 2 days	13 weeks 3 days	8 weeks 4 days 36	6 weeks 4 days	15 weeks 5 days	11 weeks 5 days 22
Sagartia lacerata (summary of all experiments)	A considerable number (not exactly recorded)	62	51 (82·3%)	3 weeks 2 days	13 weeks 2 days	10 weeks 20	4 weeks 3 days	17 weeks 1 day	10 weeks 3 days 10
Sagartia lacerata (the best experiment only)	Several	20	20 (100%)	3 weeks 2 days	3 weeks 2 days	3 weeks 2 days 4	4 weeks 3 days	8 weeks 2 days	5 weeks 5 days 4

In the above table the number in the lower right-hand corner of each of the rectangles containing an *average*, represents the number of pieces from which the average was calculated. There is no implication that specimens not included in this number failed to regenerate properly—the implication is that the time in which they regenerated could not be determined.

The essential part of these results may be better understood by their concentration in a further table as follows :—

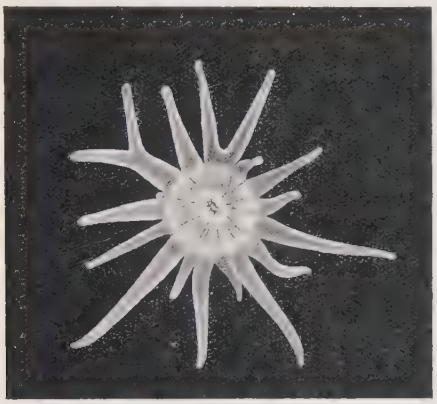
Species.	Number of pieces cut off.	Percentage reared (to nearest whole number).	Average time in which tentacles were regenerated.	Average time in which animal became fully formed.
Sagartia elegans	60	92%	4 weeks 6 days	8 weeks 5 days.
S. troglodytes var. decorata	76	29% lived 3% became fully formed	7 weeks 3 days	12 weeks 4 days.
S. anguicoma	67	58%	8 weeks 4 days	11 weeks 5 days.
S. lacerata (one experiment only)	20	100%	3 weeks 2 days	5 weeks 5 days.

These tables call for further comment. The records of the times taken for regeneration of tentacles and for the regeneration of the whole animal cannot be taken too seriously, because they are approximate, and may be partly misleading; but they are recorded for what they are worth.

Text-Fig. 9.—A specimen of *Sagartia anguicoma*, produced from a small piece cut from the edge of the base of a large specimen. Regeneration is well advanced, and the regenerated tissue is clearly distinguishable from the old tissue as a pale crescent. Tentacles were present, but were retracted at the time when the sketch was made. Magnified nearly 5 diameters.

In these regenerating pieces (except in the case of *Sagartia troglodytes*, where the regenerating tentacles are non-retractile) the tentacles are usually retractile from the beginning, and consequently may be hidden from view at the time of the periodic observations. This means that it is very difficult to tell the exact date upon

which tentacles or mouth first came into being in any given piece, and that data could not be obtained for all the pieces under observation. On the other hand, if a specimen is contracted at the time of one observation it is often expanded the next time, so that in the majority of cases the figure gained probably gives an approximation to the truth, allowing a fairly wide margin of error. The net result is that the minimum times given are probably the most valuable; the averages are probably too high; and the maximum times mean very little, since they probably represent the individuals which were either contracted most often or were abnormally backward in development. Notwithstanding the above, I think the data are sufficiently satisfactory to make valid the conclusion



TEXT-FIG. 10.—One of the two specimens of *Sagartia troglodytes* which regenerated fully from an artificially separated basal fragment. One tentacle is forked at the base, another higher up. Enlarged about 12 diameters.

that under the conditions of the experiment pieces of *S. lacerata* and *S. elegans* (the forms which lacerate naturally) regenerated more rapidly, in the main, than those of *S. troglodytes* and *S. anguicoma*.

The more important side of the result, however, is that upon which the information is precise, i.e. the percentage of pieces which were able to regenerate into fully-formed animals in the various species. Here a separate note on each form will be advisable.

Sagartia elegans.

In this species the pieces regenerate easily and often rapidly. The percentage reared (92%) is actually too low, since the remaining specimens (5) were mostly lost, and did not actually die. One can expect to rear something like 100% of any good batch of pieces detached from individuals of this species.

S. troglodytes.

The remarkable fact here emerges, that of 76 pieces, only 2 came to maturity (one of these is illustrated in Text-Fig. 10); 32 pieces made some attempt at regeneration, but in only 5 did this reach even the grade of tentacles. The regeneration was slow and obviously difficult, and often abnormal and imperfect. It is quite clear that the pieces did not regenerate at all easily under the conditions provided. This may be accounted for as follows. In the rearing of basal fragments, the probability of success depends on three factors: (1) the firmness with which the piece is attached to the glass, (2) the amount of mucus which it secretes,

Text-Fig. 11.—A fully regenerated specimen of *Sagartia anguicoma*, produced from an artificially separated basal fragment. The primary tentacles are marked I. Magnified about 9 diameters.

and (3) the degree to which it can be kept clean. In *Sagartia* the degree of firmness with which the animal adheres to foreign surfaces varies distinctly according to species, although individual exceptions may always be found to this rule. In the main, for instance, *S. troglodytes* adheres much less tightly than do *S. anguicoma* or *S. elegans*. This means that pieces cut away from *troglodytes* are often but lightly attached, or may come loose altogether; and in rearing pieces it is a rule that mortality among loose or nearly loose fragments is very much higher than among such as are well attached. Again, the amount and quality of the daily secretion of mucus in *Sagartia* varies, and this variation, of course, occurs in the fragments. *S. troglodytes* secretes a tougher and

more tenacious mucus than do *S. anguicoma* and *S. elegans*, and in the case of the fragments this often forms a dense cap or ring round the piece, from which the fragment cannot free itself, and this cap forms an admirable site for the accumulation of sediment and bacteria. To anyone who has reared such pieces these reasons are adequate to explain the difficulty of rearing *troglodytes ;* but in addition it seems in itself a delicate species, and by watching the course of regeneration one receives the impression that its regenerative ability is not strong.

S. anguicoma.

In this case, although the proportion of pieces reared (58%) was lower than in *S. elegans*, it was evident that the species possesses strong regenerative ability, and the pieces usually regenerate well and cleanly, although with less certainty than do those of *elegans*. This is doubtless partly due to the fact that they usually adhere very firmly, and secrete mucus of a less offensive nature than that of *troglodytes ;* but they seem to be also stronger and of a firmer texture in themselves. A regenerating fragment of this species is illustrated in Text-Fig. 9, and an expanded specimen fully regenerated in Text-Fig. 11.

S. lacerata.

In this species the result should theoretically be as good as those in *S. elegans*, since *S. lacerata* fragments more freely in nature than any other form. In fact, however, except in the best experiment, they fell below expectation ; but it is possible to account reasonably for this. In the earlier experiments, most of the pieces cut off were very small (*S. lacerata* is usually a small species, and they were mostly smaller than in the other species used), and did not regenerate very well. I believe this may be due to the fact that laceration in this species, when it occurs naturally, is a gradual process of constriction, and does not involve a large open wound as does the ripping incurred by *S. elegans*. In a small piece cut off suddenly, on the other hand, a wide open wound is involved, and this does not seem to suit the species. Consequently, after this had been realised, 20 pieces of slightly larger average size, but still not more than a few millimetres in diameter, were cut off from a set of adults, and all of these regenerated and survived.* Taking all the experiments together the percentage is lowered to 82%, which even then is higher than in *S. anguicoma*.

Conclusion.

If " outside " water in quantity had been available, probably a higher percentage of pieces of *S. troglodytes* and *S. anguicoma* would have been

* It is just possible (but not probable) that one or two of these pieces included tentacles when first cut off.

reared than in tank-water; and probably the same would be true in nature. This consideration notwithstanding, the marked differences which occurred under identical conditions in the four species certainly mean something, and it may be concluded that the regeneration of pieces takes place more readily in the species which lacerate in nature than in those which do not. At the same time those which do not naturally lacerate are *able* to regenerate from fragments, though to a different degree in different cases. This renders the more remarkable the fact that they do not normally lacerate in the wild state.

4. EVIDENCE DERIVED FROM THE LITERATURE.

It is hardly necessary to give a complete summary of the data available in the literature which bear on the subject at issue, for reasons which will appear (note on exceptions, in Section 7). I give, however, a selection of facts extracted from the considerable amount of literature which exists on the subject. Some of these supplement my own results, especially in the cases of *Diadumene luciæ* (where my results are scanty) and *Cereus pedunculatus*. The other extracts are designed to illustrate the type of observations which have been made by other authors.

Fission, laceration and regeneration in Actinians have been studied by a number of authors—by Carlgren, Dalyell, Andres, Cary, Davis, Child, Parker, Hammatt, Torrey, Hazen, Loeb, and others. Many of the observations of these authors are relevant to the present question, although the aim of their studies has usually been distinct from that of this paper. Several of them, for instance Dalyell, Carlgren, and Davis, have clearly realised that in forms with which they were dealing a stated method of reproduction was characteristic of given species. The data quoted below, from Dalyell, makes this evident, in his case. Carlgren, in his 1904 paper on regeneration, deliberately selected for certain experiments species which do not habitually reproduce asexually, in order to avoid the introduction of complicating factors into his work; and in many other ways it is clear that he is aware of the state of affairs. The present paper, however, is the first study, as far as I know, devoted to the consideration of the specific value of reproductive methods as such.

The observations made in his aquarium by Sir John Dalyell possess great value, and the following data, extracted from his *Rare and Remarkable Animals of Scotland*, concern us here.

Actinia equina. Specimens were kept in captivity for as long as 13 and 20 years. Dalyell was fully aware that the normal habit of the species is to produce viviparous young; he also observed the production of embryos prior to metamorphosis, but these were rarely liberated by the parent, and such an occurrence was regarded by Dalyell as accidental and

non-typical. One specimen in his possession for 20 years produced 334 young during that time ; another which he kept for over four years produced 200 young in 14 days. The first of these specimens produced further young after Dalyell's death (see Ashworth and Annandale, 1904). In other cases young individuals were reared. One of these first produced viviparous young when between 14 and 15 months old, and by the time it was 4 years old had produced 64 of them. Another lived for nearly 5 years ; at 3 years old it had produced 28 young, the first of which had appeared at between 13 and 14 months ; subsequently it produced many more, 7 one night and 15 another. A third produced its first young at a year old, produced 60 in three years, and more afterwards ; this one lived 10 years. A fourth began to breed at 14 months old, and was prolific ; two depositions of young containing 60 and 43 respectively ; this specimen, a double one, was accidentally torn in half at about six years old, and one half produced further young after this. In this species viviparity has also been observed by many other workers.

Sagartia elegans. Here there is an observation made by Dalyell to the effect that specimens kept by him for three years produced no viviparous young ; this confirms my own and Evans's results.

S. troglodytes (the " *Actinia explorator* " of Dalyell). Dalyell was aware that this species is viviparous, and records the production of over 60 young in a night by two small specimens.

S. lacerata. In the case of this species Dalyell showed that laceration is the characteristic mode of reproduction. On page 228 he remarks : " Amidst the numerous embarrassments obstructing the discrimination of species and varieties of the Actinia " (i.e. of Actiniæ), " it is fortunate to meet certain immutable features, so prominent as to distinguish some of them, so definitely from all others, as to leave no liability to error." This remark refers, partly at least, to the habit of laceration. One of Dalyell's specimens produced over 70 young by laceration in the course of a year, and one laceration which was reared began to lacerate itself after nine months, and produced 40 lacerations in 80 days. Specimens were kept for over three years ; no viviparous young were ever observed. Lacerations sometimes achieved tentacles 15 days after the appearance of the basal irregularities which produced them.

Finally, Dalyell realised that among anemones the animal " propagates by two distinct fashions, as seen in different species "—this refers to viviparity and laceration by constriction, other methods (apart from the production of ova) not having come to his notice.

Next we may consider a paper by Davis (1919) on asexual multiplication and regeneration in *Diadumene luciæ*. This paper deals mainly and in detail with the morphological results of fission, but a large amount of material was used by the author, and it emerges clearly from his study

that longitudinal fission involving the tearing of mouth and throat is a characteristic and frequent occurrence in the species; and the author remarks on page 167: "There is no suggestion of a division resembling that known as basal fragmentation. Any other method of asexual reproduction than that described above" (i.e. fission), "must be very rare in the adult form of this species." That fission is habitual in the species is confirmed from various quarters, by the observations of Davenport, Hargitt, Hausman, Walton, etc., as well as those of Evans and myself. It has also been suggested that the species can bud and lacerate (Davenport 1903, Hausman 1919), but these suggestions are not, so far as I know, founded upon actual observations, and if they are correct these processes must, as Davis remarks, be quite exceptional.

In 1911 Cary published a paper on pedal laceration in Actinians, giving an account of this occurrence in *Cylista leucolena* and in three species of *Aiptasia* (none of these forms is British). Among 1300 specimens of *C. leucolena* examined, 1234 had given rise to lacerations; the same is true of 78 out of 150 specimens of *Aiptasia pallida*, of 187 out of 220 of *A. tagetes*, and of 20 out of 52 of *A. annulata*. For details reference should be made to the paper.

The observations made by Miss Jessie Nelson, and later by Ashworth and Annandale (1904), and by Evans, on some specimens of *Cereus pedunculatus*, are interesting in this connection. The specimens in question are 16 in number, and have now been in captivity for some 66 years; their actual age must be at least 70 years, and may be considerably more. These specimens (referred incorrectly by Ashworth and Annandale to *S. troglodytes*) are still in good health, and during their captivity have produced countless viviparous young, some of which have been reared and have been prolific in their turn, which applies again to the grandchildren. The original specimens are mostly still breeding freely, and have never, so far as I know, produced anything but such young.*

Further papers dealing with asexual reproduction and regeneration are enumerated in the list of literature at the end of this paper, and the case of *Metridium* is mentioned on page 162. The above examples will serve to illustrate the sort of material which may be gleaned from the literature, and the only other point which need be noted at the moment is that there exist records which contradict the conclusions of this paper; these are dealt with on page 161.

* One of the original specimens was removed from the tank containing the others on May 27, 1925; in the 123 days succeeding its isolation it produced 102 young. Since then it has produced none up-to-date (May, 1928). This suggests that it had been fertilised from sperm of another individual before isolation—although no emission of sperm had been seen. Some specimens of the species are undoubtedly hermaphrodite, but it does not follow that it is self-fertilising.

5. THE EFFECT OF THE MODE OF REPRODUCTION UPON THE MORPHOLOGY.

A considerable body of knowledge exists as to the effect of asexual reproduction on the morphology of Actinians, and as to the morphological conditions which follow the regeneration of artificially separated portions of these animals. For details reference must be made first and foremost to the very important papers of Carlgren (1904, 1909, 1909a), and also to that of Davis (1919) above mentioned, as well as those of Cary (1911), Davenport (1903), Hargitt (1914), Parker (1897, 1899), Torrey (1898, 1902), Hammatt (1906), A. F. Dixon (1888), G. Y. and A. F. Dixon (1889 and 1891), Hahn (1905), etc.

The point I wish to make here is that there is quite enough evidence to show that anemones with more or less irregular symmetry (i.e. those which depart from the typical condition possessing 2 siphonoglyphs, 2 pairs of directives, 6 primary pairs of mesenteries, and 6 primary tentacles, all bilaterally arranged) are generally specimens which in one way or another have been produced asexually. These specimens may have a varying number of siphonoglyphs and directives, a number of primary tentacles and mesenteries other than six (4, 5, 7, 8, 9, 10, 11, 12, 13, 14), and no definite bilateral symmetry. This is the general rule; but it does not imply either (a) that asexually produced specimens are never hexamerous and bilateral, nor that (b) sexually produced specimens are never irregular. Both these conditions do exist, for specific causes. But our knowledge is sufficient to make it a very probable assumption that if, in any given species, a high proportion of the individuals exhibit irregular symmetry, this is a species in which asexual reproduction is frequent. If, in such a case, we have even a few actual records of asexual reproduction, the assumption that it is general becomes still more likely. Conversely, the result of my own and other observations shows that in the case of viviparous species the young are normally symmetrical and hexamerous; so, consequently, are the adults; and if, in a species whose reproductive habit is not known, the adults are found to be regular and hexamerous, it is probably one in which either viviparity or at least the absence of asexual reproduction is prevalent. There do arise cases in which individuals of sexual origin are irregular; but this can be due to reparation of injured parts and similar causes, and does not affect the general rule. My own study of a wide range of material has shown that the above remarks apply to the species specially dealt with in this paper—i.e. in *Sagartia elegans*, *S. lacerata*, *S. sphyrodeta*, *Diadumene luciæ*, and *D. cincta*, the adult symmetry is often or usually more or less irregular, whereas in *S. troglodytes*, *S. anguicoma*, and *Cereus*

pedunculatus (viviparous or oviparous forms) the symmetry is normally regular and hexamerous. In this latter connection it may be noted that in a paper published in 1898, Clubb records an anatomical examination of 165 specimens of the viviparous *Actinia equina*. All of these were hexamerous; and 158 of them were bilaterally symmetrical, with 2 syphonoglyphs and 2 pairs of directives.

6. REPRODUCTION IN THE BRITISH SPECIES AS A WHOLE.

I am at present unable to give a complete collection of records of reproduction in British species from the literature, because I am on the eve of departure for a year's research in Australia; but in the following list I give a contribution towards these records, from the observations of Evans and myself. In some cases the data given are merely additions to, or confirmation of, facts already known; in others the data are new. The letters E and S indicate whether the observation is due to Evans or myself; and species in which we have seen no reproduction are not included. "Sperm, 2.27" means "Sperm emitted, February, 1927"—and so on.

Gonactinia prolifera. Transverse fission (S).

Milne-Edwardsia carnea. A young specimen taken from a Ctenophore (*Bolina* sp.) upon which it was parasitic, in October, 1926, was reared by Miss Delap, of Valencia, and sent to us. We both confirm it as this species, having seen it alive and sufficiently grown for an accurate determination. We have also seen young specimens creeping about stones inhabited by the adult.

Halcampa chrysanthellum. Sperm, 2.27 (S).

Ilyanthus mitchellii. Ova, 26.10.26; 9.27 (E). The ova are extremely large.

Actinia equina. Viviparous young habitual (E and S).

Anemonia sulcata. Longitudinal fission, 25.9.22; 28.4.24; 2.4.25; 1.9.23 (E).

Bolocera tuediæ. Ova, July, 1925, and in 1926 (E).

Tealia felina. Sperm, 5.11.22. etc. (E).

Bunodactis verrucosa. Viviparous young habitual (E and S). A brood of 27 young (produced under the action of menthol) was seen, 30.5.27 (S), the same individual producing more young later. This specimen and some of its young are illustrated in Text-Fig. 5.

Anthopleura thallia. Longitudinal fission frequent (E). The prevalent irregular symmetry of this species supports these observations.

Diadumene cincta. Laceration by tearing fairly frequent (E and S).

D. luciæ. Longitudinal fission habitual (E and S).

Aiptasia couchii. Transverse fission, 10.25 (E); viviparous young, 8.25 (E).

Metridium senile. Laceration habitual (E and S). Ova, 4.8.22; sperm and ova at other times (E).

Calliactis parasitica. Sperm, 9.22 (E).

Adamsia palliata. Ova, 29.10.25, and on several occasions since (E).

Cataphellia brodricii. Viviparous young in quantity from specimens collected at Salcombe and Wembury (Devon) in March and April, 1927. Several adults produced young, the total number of the latter amounting to 231; the three largest broods contained respectively 68, 85, and 51. Since the adults and young are normally regular and hexamerous, it is probable that viviparity is habitual (S). Specimens sent to Edinburgh at the time mentioned produced further young individuals afterwards (E).

Hormathia coronata. Viviparous young, 15.3.25; 7.5.25; 10.6.25; 7.4.27 (E). The species is normally regular and hexamerous, and there are French records which state that it is viviparous; probably, therefore, it is habitually so.

Paraphellia expansa. Ova probably belonging to this species have been seen (E).

Gephyropsis dohrnii. Laceration, 15.11.25 (E), and at other times (S).

Sagartia elegans. Laceration by tearing habitual (E and S).

S. anguicoma. Sperm, 11.25 (E).

S. troglodytes. Viviparity habitual (E and S). Sperm, 11.6.22; ova, 9–10, 6.23 (E), and at other times (E and S).

S. lacerata. Laceration by constriction habitual (E and S).

S. sphyrodeta. Longitudinal fission habitual (E and S).

Cereus pedunculatus. Viviparity habitual (E and S).

Phellia gausapata. Laceration observed in each of 5 specimens; one or two lacerations produced by each (E).

7. DISCUSSION.

It has been sought to establish that

(1) In the species selected for study, the deposition of ova may occur in any of them (except that in *Cereus pedunculatus* the ova normally, and perhaps always, develop within the cœlenteron of the parent).

(2) Apart from this, there are two principal methods of propagation in these species, viviparity and asexual reproduction; and only one of these methods normally occurs within a single species.

(3) In the forms which reproduce asexually, only one out of three possible methods (total longitudinal fission, laceration by constriction, or laceration by tearing) normally occurs in any one species.

Can the above statements be regarded as proved ? In this connection the following points may be noted.

(1) It is a striking fact that there is not, in my experiments, a single exception of any kind to the rules postulated. The same applies to the observations of Evans, and to my own general experience of living anemones, which has spread over some fourteen years. This distinctly enhances the results. The most difficult point to establish is the negative observation that certain species do *not* reproduce asexually ; but since asexual reproduction occurs at any time of the year, and fairly freely where it does take place, there should have been at least some exceptions if a negative conclusion were incorrect.

(2) There are other series of data available beyond the experiments, which confirm the above results.

A. Observations by various workers recorded in the literature. It so happens that in some instances where my own results are scanty, the gap can be filled either from the literature or from Evans' observations.

B. There are data available relating to the morphology of considerable numbers of specimens of many of the species concerned, which add confirmation to the experimental results.

(3) For the above reasons I believe that, although my experiments taken alone would be insufficient to prove the case, when all the available data are taken into account, the conclusions outlined above are justified. Moreover, I have reason to think that the numbers yielded by my experiments understate the case rather than otherwise, since the processes observed went on rather more slowly under the Plymouth conditions than has been the case with many of the specimens in Evans' aquarium.

The question of exceptions must be next considered. I do not wish to maintain that in any species such never occur ; they may well do so, even though they have not come under my notice ; but even if they do, the general contention is not invalidated. In species which have *not* been specially studied here, moreover, it may be true that different conditions occur, and that combinations not represented in those here selected are present. It is quite possible that just as in morphology it is found that some species are stable and others are unstable, so in the matter of reproduction it may be true that some species (such as those investigated) are stable or almost stable, others more variable. I suspect that Metridium may be somewhat variable in this respect, although laceration is certainly its prevalent method. Again, in *Aiptasia couchii*,

although we do not know enough about the species to be sure what are its normal habits, it appears to be established that the species is viviparous and that it also undergoes, at times, a curious form of transverse fission.

Nor must the possibility be forgotten that within the same species the method of reproduction may vary with locality. I am not aware that this applies to any of the British species within the British area, but it *may* apply, for instance, to their Norwegian or Mediterranean representatives. In the case of *Actinia equina*, Gravier has found that the species is still viviparous at the island of S. Thomé, near the Equator. In *Sagartia troglodytes*, however, the viviparous habit has not been observed by Carlgren in Scandinavian waters (this species is in any case oviparous as well), although of course it may occur. Carlgren's observations on *S. troglodytes* confirm my own, that it does not reproduce asexually, and the same applies to *S. viduata*, a northern species closely allied to *S. anguicoma*.

There are a number of records in the literature which definitely contradict my observations. It is very difficult to tell whether these have any serious bearing on the question, because frequently either sufficient precision is lacking in the records, or they apply to isolated instances only. It must be remembered that the phenomena exhibited by Actinians have not always been understood at all clearly. When, for instance, we are told that in some species *budding* has been observed, it is much more likely that what was actually seen was either a subsidiary tuft of tentacles (sometimes including a disc and throat as well) on the side of the anemone, produced as the result of a small wound, or as the consequence of the regeneration of an atypical laceration ; or some other similar phenomenon. Such formations resulting from wounds certainly do occur, and have nothing to do with asexual reproduction. Some records of " buds " are due to a regenerating laceration which has not been fully detached from the parent. True budding is probably very rare among Actinians, if it occurs at all. Again, at one time it was generally assumed that double-headed anemones, or specimens with two bases, were necessarily stages in fission. Carlgren and others have shown that permanent double-monsters *can* originate from arrested and incomplete fission ; but that many of them are double from an early embryonic stage, or arise from some other reason, and their condition has nothing to do with ordinary asexual reproduction.

Further, in the early days an isolated record of the production of viviparous young, in the species in which we know that they do not normally occur, might well apply to basal fragments which had not been noticed until they had formed tentacles. When, as was often the case, the actual birth of the young was not witnessed, this is the probable

explanation, and I know of one instance in which it actually occurred. In other cases records are rendered valueless because we cannot be certain that the specimens under observation really belonged to the species to which they were assigned; several species of Sagartia live in the same localities and have often been confused one with another. For the above reasons, although I am aware, to give instances, that viviparity has been recorded in *S. elegans* (Gosse 1860, pp. 46 and 71), that laceration has been recorded in *Actinia equina* (Landauer 1924), *Cereus pedunculatus* and *Bunodactis gemmacea* (Andres 1881), and so on, I am confident that the majority of such records are either mistakes, or that they refer to the results of injury, to double individuals, or to similar conditions. Some of them, no doubt, refer to genuine exceptions, but there is no evidence to show that these exist in sufficient amount to invalidate in any way the conclusions of this paper. Such records for the genus Sagartia are but few.

The case of Metridium is worthy of a little further attention, since much research has centred round it. Papers dealing partly or entirely with Metridium have been published by Carlgren (1904, 1909), Verrill (1922), McMurrich (1901, 1911), Hausding (1914), Parker (1897, 1899), Torrey (1898, 1902), Hammatt (1906), G. Y. and A. F. Dixon (1891), Hahn (1905), etc. Carlgren, Parker, Torrey, and Hahn especially have studied the influence of asexual reproduction on the morphology, among them giving many details of variation in siphonoglyphs, number of perfect mesenteries, and general symmetry, and dealing with the question of double-monsters, etc. Torrey (1902) emphasises that although fission and budding occur in the species, neither of these has more than a trifling influence on the number of individuals, since laceration is frequent, rapid, and universal. Among 2662 individuals, less than 2·5% were suspected of fission or budding, and if the origin of the so-called "fission" and "budding" could be fully studied it would doubtless be found that many or most of the instances were really due to double-monsters, injuries, etc. Double specimens are normally permanently double and the halves do not separate. Whether fission of the type found in *Sagartia sphyrodeta* occurs at all in Metridium is doubtful. Consequently, although there may be more variation in the reproductive processes here than in other cases, there is certainly less than might at first sight appear. (The above remarks refer indiscriminately to *Metridium senile*, *M. fimbriatum*, and *M. marginatum*; it is held by some authors that these are all the same, by others that they are not. The question is not finally soluble at the moment.)

Lastly, I would like to make a comment on the situation; but wish to make it quite clear that the following remarks make no claim to

represent a discussion of the species-problem in general. I hope to discuss this problem at a later date ; but for the moment I am giving an indication of the sense in which the word " species " is here used, in order that the facts concerning methods of reproduction as specific characters may be fitted into their place with relation to our existing knowledge of species.

There exists, as is well known, an unfortunate division of zoologists into systematic and general workers. Systematic work is regarded, not without reason, by the ordinary zoologist, as at the best a necessary evil, and it is hardly possible to mention the word " species " without causing an unfavourable reaction in one's audience ; the very word conjures up visions of dullness. For this state of affairs the systematists cannot be held guiltless, since their work represents, only too often, a purely academic study of certain aspects of organisms, and is divorced from any general interest in the field of zoology as a whole. On the other hand, it is unfortunate that the question of species receives as little attention as it does from zoologists in general. The subject of evolution is one of the central problems of biology, and it is a problem which is intimately bound up with that of species. It will hardly be denied by anyone that work which sheds light upon the question of evolution is a live issue. At the present time, when experimental methods of research are so much to the fore, there is an excellent opportunity for a fresh attack upon the species-problem, from an angle distinct from the classical one. It is not enough to " leave it to the systematists," since this will not lead to any advance in our knowledge ; the field must be explored by biologists with general knowledge and interests.

If, then, we are to approach the problem along new lines, one of the steps which must first be taken is this, that species must be studied intensively, and everything about them must be taken into account. Not only must we know that A differs from B in the possession of a different number of hairs on its legs, but we must also know the whole of its morphology, its life-history and habits, its methods of reproduction, and whether it possesses distinctive physiological characteristics unlike those of B. When this has been done we shall at least know more about the potentialities of species than is at present the case.

At this point there arises the question " What is a species ? " This is a matter of definition too involved for detailed discussion in the present paper, but it will be advisable to give some indication of the sense in which the term is here employed.

The Actinians which have been specially studied here present a case in which, despite the general belief to the contrary, it is possible to recognise the species (from living specimens) quite distinctly by taking into account morphology, markings, and colouration ; and no specimen

comes to hand of which one cannot say "this anemone belongs to such-and-such a species, and it is clearly different from any other kind of anemone." So much is this the case, that it is often possible to identify an anemone from a detached fragment of its basal margin.

For the purposes of the present stage of this discussion, therefore, the word "species" may be regarded, in the first place, as a term covering all existing specimens of any animal which is not of the same kind as any other animal; the criteria of distinction being a series of differences which are visibly expressed throughout the entire morphology. But since the factor of time must also be considered, this definition requires the qualification that a species now living also includes many individuals which are extinct, and many which are yet to come. Its limits in time lie between

(a) The time when the animal type in question first became recognisably distinct from any other.*

(b) The time when this same type, by splitting up into others, or by becoming extinct, will cease to exist as such.

Hence, it is clear that a species, although it may persist for a long time, is transitory. Moreover, if it is one which is to split up ultimately into others, there will be a period at the beginning and another at the end of its history during which it will be difficult to distinguish it from parallel or derived forms. Consequently, the limits of a species *in time* can never be precisely fixed, although its morphological limits for a certain period of its history may be sharply marked. It may be true, moreover, that at the present time a number of species are not in the phase of evolution during which they are recognisably distinct, as in the case of the Actinians in question, but are in a state of flux. If such forms exist, one would expect to find groups of forms, evidently allied, among which races (linked perhaps by numerous hybrids) can be distinguished with more or less accuracy, but among which the species cannot be determined with the degree of precision which is practicable among the anemones. I feel that such an explanation may account, for instance, for the state of affairs which prevails in the genus Dactylorchis, a group of plants which I have studied somewhat extensively in the field. If, therefore, there are cases in which it is possible accurately to determine specific limits, and others in which it is not possible; and if in any case the limits of a species in time are not sharply marked; it is evident that the conception of a species is at present lacking in precision. But in the following paragraphs the word may be understood to mean, as nearly

* By "recognisably distinct" is meant "distinguished by a series of differences which are visibly expressed throughout the morphology"; i.e. recognisably distinct as an animal type from any other animal type. In other words, although a red animal is "recognisably distinct" from a black one (and the difference may depend upon a Mendelian factor), this does not necessarily mean that the two are specifically distinct.

as the above qualifications will allow, an animal type which is different from all other animal types.

Having explained the interpretation to be placed upon the word "species" for the purpose of this discussion, it may next be pointed out that, in the methods of reproduction which have been studied in these anemones, we have a criterion for specific distinction of a nature different from the usual morphological standard. It is evident that in dealing with a sharp distinction between a species which does, and another which does not, habitually reproduce asexually, we are dealing with a marked difference between the physiological constitutions of the forms in question. The fact that any species *can* regenerate from artificially separated fragments merely renders more striking the apparently complete abstinence of certain species from doing so. Now, in the species in question there is no doubt about the morphological distinctions between them; but we can hardly speak of a reproductive method as "morphological." It is true that morphological distinctions are the expression of different series of physiological processes, and that the "morphological" and the "physiological" are interdependent, and merge into one another when philosophically considered; but for ordinary purposes of terminology it is necessary to draw a line between the two, and a method of reproduction must lie on the physiological side of that line.

This raises the question of "physiological species" in general. In this connection it may be noted that in the higher animals (e.g. the mammals) the morphological differences between species may be considerable, whereas marked physiological differences of a grade comparable to the differences in reproductive physiology exhibited by the anemones, are not present. The interest of the anemones lies in the fact that among them there may exist side by side a slight degree of morphological distinction between two species, accompanied by a very marked physiological difference. If, in this respect, it is true that the anemones represent a stage intermediate between the highest and the lowest animals (as indeed from general considerations might be anticipated), we should expect to find that on a still lower grade there might be morphological identity between species which would then be distinguishable only by physiological tests; and this state of affairs appears to be realised, for instance, in the bacteria and in the moulds. To such cases as these last, the term "physiological species" may very appropriately be applied; but it should be remembered that such species are of the same essential nature as those which occur among anemones or mammals, whether the criteria which most readily distinguish them be morphological or physiological. In other words, so long as a species is understood in the sense of this discussion, it is immaterial whether the adjective

applied to it be "morphological" or "physiological." It follows from this, that the word "species" should not be applied to cases in which it is possible, within the limits of a single species (in the accepted sense), to distinguish groups of individuals (e.g. blood-groups) which exhibit different physiological reactions of certain kinds. Such differences as these (which can be paralleled on the morphological side) do not necessarily indicate specific difference at all. It may be that some of them are the forerunners of far-reaching changes which will in time differentiate one species into more than one; but until such differentiation has taken place these groups cannot validly be termed species.

The addition of the bacteria, etc., to the list of organisms amongst which species can be recognised, involves the emendation of the definition of a species given below, to the effect that the criteria which distinguish organisms of one kind from those of another may be physiological instead of morphological.

In conclusion it may be noted that the case of the Actinians is not an isolated one. In Ascidians, as Berrill (1928) has shown, species may be distinguished according to whether or not they have a tadpole-stage in their development. In regeneration among invertebrates, distinct methods of behaviour after injury, characteristic of species, are probably widespread, as demonstrated, for instance, by the work of Nusbaum and Oxner on Lineids. In the anemones themselves, there are specific differences in the power with which the base adheres to foreign substances; in the quality and amount of mucus which the animal secretes; and in its irritability—e.g. in the readiness with which it will shoot forth acontia when provoked. These last-quoted cases, however, are much less sharp and less easily measurable than the methods of reproduction; and they may vary very considerably from one individual to another, and according to the type of environment which an individual has inhabited, prior to collection. They are, in fact, differences of tendency rather than absolute distinctions such as method of reproduction, mode of early development, or behaviour during regeneration.

8. SUMMARY.

1. Eight species of Actinians (enumerated on p. 148) have been specially studied with regard to their reproductive processes.

2. Among these forms five methods of reproduction occur—longitudinal fission; laceration by tearing; laceration by constriction; production of young viviparously; deposition of ova.

3. Deposition of ova may co-exist with any other method, except perhaps in certain viviparous forms.

4. Apart from this, one method only prevails in any one of the selected species—

A. Longitudinal fission in *Sagartia sphyrodeta* and *Diadumene luciæ*.

B. Laceration by tearing in *Sagartia elegans* and *Diadumene cincta*.

C. Laceration by constriction in *Sagartia lacerata*.

D. Viviparity in *Sagartia troglodytes* and *Cereus pedunculatus*.

5. In *Sagartia anguicoma* neither viviparity nor asexual reproduction occurs.

6. The viviparous forms studied do not reproduce asexually; nor are those which reproduce asexually viviparous.

7. In the experiments and observations of the author and of W. E. Evans, no exceptions to the above statements occurred. The question of exceptions is discussed on page 161.

8. Four of the above species were selected for regeneration experiments. Pieces were cut off from the margin of the base in each (artificial laceration).

9. In *Sagartia elegans* (which lacerates naturally) it was found that nearly 100% of such pieces would regenerate easily; in *S. lacerata* the same was true in the best experiment.

10. In *Sagartia troglodytes* (which does not lacerate naturally) only two pieces out of 76 regenerated fully, and the regenerative ability of the species appeared to be weak. In *S. anguicoma*, however, the percentage of pieces which regenerated fully (and did so strongly) was very much higher, though not reaching that of *S. elegans*.

11. Regeneration was probably more rapid, in the main, in the species which lacerate naturally than in the others.

12. It is maintained that sharp distinctions between species, such as those mentioned above, are of interest from the point of view of the general problem of species.

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On the Nematocysts of Sea Anemones.

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With 1 Plate and 10 Figures in the Text.

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INTRODUCTION.

The main object of this paper has been to determine whether or no it is possible to differentiate the species and genera of Actinians by employing as criteria the characteristics of their nematocysts.

I wish to acknowledge that I have received a grant from the Royal Society which has very greatly assisted the work described. The figures in Plate I have been published before in my Ray Society monograph on the British anemones; but their repetition here is essential for the adequate illustration of this paper. Figs. 1 and 4 on this plate are copied from Will's paper on spirocysts (1909a, Pl. 3, Figs. 4 and 9).

1. MATERIAL AND METHODS.

The material for this study was mostly obtained at Plymouth, this being supplemented by specimens from other places where necessary. The whole of the observations apply to fresh material studied before fixation, unless otherwise stated.

The object of the research was to take measurements of the capsules of nematocysts and to make observations on the distribution of the

different patterns of nematocyst among various species ; for this purpose it was not necessary to make permanent preparations, and such were not attempted.

When the nematocysts to be studied are contained in an acontium belonging to a species which emits acontia readily, or when they are situated in a tentacle, it is easy to isolate a small piece of one of these tissues for study. Similarly, if a sample of nematocysts from the body-wall be required, a small amount of ectoderm containing them can readily be scraped off. If, however, nematocysts are required from the mesenterial filaments, throat, peristome, acrorhagi, etc., it is advisable to anæsthetise the anemone with menthol, until it ceases to respond to tactile stimuli. It can then be cut up without undue contraction, and accurate samples of the tissues required may be extracted.

For purposes of measurement and general observation fresh preparations of nematocysts may usually be employed without staining. In certain cases, however, and for the observation of particular details, these preparations may be stained directly. The best stains for general purposes are methylene blue (a 1% solution, or weaker) and acid fuchsin (1%). Spirocysts have a strong affinity for acid fuchsin, and some kinds of nematocysts, or perhaps all nematocysts under given conditions, for methylene blue—and it is possible to stain a preparation containing both so that the spirocysts appear bright crimson, and the nematocysts deep blue ; usually, however, the stains are employed separately. I have tried various other stains—picronigrosin, hæmatoxylin, eosin, picro-indigo-carmine, methyl green, neutral red, Janus green, etc. Some of these are useful for staining nematocysts or spirocysts in sections, but for fresh material nothing I have used equals the methylene blue and fuchsin ; other workers have found the same. In some cases the details of the barbs and spirals on the threads of the nematocysts can be seen to more advantage by introducing them into a medium of high refractive index. A medium which I have found serviceable is one described by Lee (*Microtomist's Vade-mecum*, 1921 Edition, p. 224)—a saturated solution of potassium iodide and biniodide of mercury in distilled water. The solution is made by grinding up the two materials together with a little water in a small mortar ; the amount of these which dissolves in a small quantity of water is considerable, and a syrupy solution of a clear greenish yellow colour results. This solution can be either used at full strength or in various dilutions, according to the index required. When adding it to a fresh preparation it is best to acclimatise this by introducing a drop of a dilute solution before a higher concentration is used. The action of methylene blue for the demonstration of detail is altered and sometimes enhanced by the addition of a very little potassium hydroxide (in a 5% or 10% solution) to the preparation. If the mercury

medium is also employed, this should be added after the KOH and methylene blue, which may with advantage be mixed (provided proper proportions are used) immediately before they are added to the preparation. The results with such preparations are sometimes excellent, but very transitory.

Fresh preparations are made as follows. A small piece of the tissue to be studied is placed on a slide in a drop of sea-water. It is chopped into very fine fragments with a small needle-knife. All fragments are then eliminated save those of the finest grade, and a cover-slip is added. The cover-slip should be a large one, almost completely covering the slide, and the drop of fluid beneath it should be small. This ensures that the film between slide and cover-slip shall be very thin, so that the cover-slip is held tightly down. Consequently the nematocysts in the preparation do not move about in the fluid ; they cannot, of course, be measured unless they are perfectly stationary. After the addition of the cover-slip, the preparation may be further dissociated by holding the slip down at one corner, between finger and thumb, and rubbing its surface firmly with the blunt end of a small scalpel, especially over the spots where little masses of tissue occur. In good preparations of this nature there should be many isolated nematocysts both exploded and otherwise, free from surrounding tissue. The smaller the amount of tissue used the better—sometimes it is enough to rub a fragment of tissue in a drop of water on a slide, remove the tissue, and use the nematocysts left in the drop. Larger masses of tissue, dissociated by being firmly pressed out, are useful for certain purposes, but not if one desires to see detail in the capsules. The method here outlined is not a refined one, but quite adequate for the object in view.

The microscope employed for the work was a Leitz binocular, with interchangeable binocular and monocular body (the monocular being used for measuring). It was used with a thorium-lamp, achromatic condenser, and a bull's-eye between the lamp and the mirror. Various objectives (oil-immersions) and eye-pieces, including compensating-oculars, were tried, but for general purposes it was found that No. 2 eye-pieces and a 10 water-immersion objective (Leitz) gave the best results.

2. ACCOUNT OF THE OBSERVATIONS MADE.

The measurements recorded below were made with a Leitz eye-piece-micrometer, No. 2 eye-piece, and 10 water-immersion objective (very rarely a $\frac{1}{12}$ inch oil-immersion).

A cnida, be it a nematocyst or a spirocyst (see p. 187 for further details), consists of a hollow refringent capsule, with one end of which a hollow thread is continuous. The thread is inside the capsule before explosion takes place, outside afterwards ; and in changing from one

A
B
C
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position to the other it evaginates or turns completely inside out, as one may turn a glove-finger. The dimensions of the capsule are less variable and much easier to obtain than those of the thread, and are therefore taken as the standard of size.

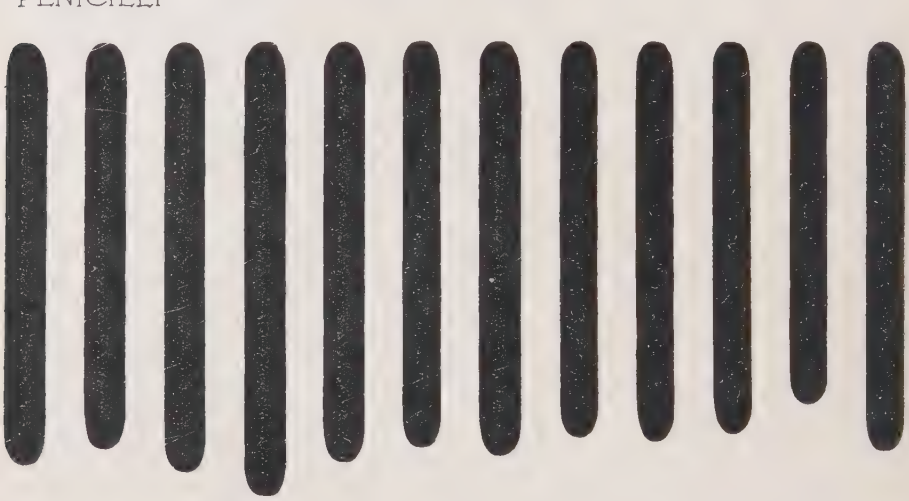
All the measurements given below, therefore, refer to the capsule, measured on fresh preparations in sea-water (unless otherwise stated), unstained and free from reagents, so that no distortion of the natural dimensions has been introduced. The capsules were measured after the eversion of the thread, wherever possible, because it is always easier to recognise the pattern of a capsule after evagination than before, and thus one avoids any question of confusing two similar kinds. In certain cases, however, the capsules seem to explode reluctantly, and a large proportion of evaginated specimens cannot be obtained without the use of reagents ; in such cases they were measured unexploded. In these instances, of course, care was taken to ascertain the exact appearance of the type of capsule in question both before and after evagination, so that no question of confusing types is involved. The latter becomes more important in dealing with fixed material. In the tables on pages 192–198, therefore, the measurements are on exploded capsules, unless otherwise stated. A comparison of exploded and unexploded nematocysts will be found on page 198. The margin of error in the measurements is probably very slight as regards the *length* of the capsule, but greater in the case of the breadth, which must be regarded as approximate. The number of samples of any one tissue examined was usually 2 or 3, sometimes more ; a single sample was used only in cases where very little material was available.

It should be noted that all the statements in this paper refer to the types of nematocysts which *predominate* in any tissue. In many cases there exist, in one and the same tissue, majority-forms and minority-forms. The latter are usually smaller than the former, and although they are sometimes rather numerous, they are generally present in much smaller numbers than the majority-forms. It is difficult to estimate their numbers and importance, and also to make out their structure, and in the present study they have been left out of account. In adequate fresh preparations there is no difficulty in determining which are the majority-forms.

Text-Fig. 1.—Sketches showing the general appearance of some Actinian nematocysts (for more detailed drawings see Pl. I). Figs. A, B, C, and F are penicilli of different varieties ; the others are spirulæ, their barbs erect in some cases, reversed in others. Fig. H (*Metridium*) is a spirula, but only the enlarged basal part of the thread is shown, this part being unusually long here. A, *Sagartia troglodytes* var. *ornata* (acontium) ; B, *Phellia gausapata* (tentacle) ; C and K, *Phellia gausapata* (acontium) ; D and G, *Gephyropsis dohrnii* (acontium), two nematocysts of the same kind in different conditions ; E, *Paraphellia expansa* (acontium) ; F, *Peachia triphylla* (mesenterial filament) ; H, *Metridium senile* (acontium) ; M, *Peachia triphylla* (throat).

A. Variability of the Capsules within a single Species.

The first step was to gain some idea of the degree to which the size of the capsule varies in a single tissue of one and the same species. For this purpose a variable species (*Sagartia elegans*) was chosen, and the nematocysts from the acontia of specimens from different localities (Plymouth and Valencia) were studied. Twelve specimens were used, belonging to various colour-varieties (*venusta*, *venustoides*, *nivea*, *niveoides*,



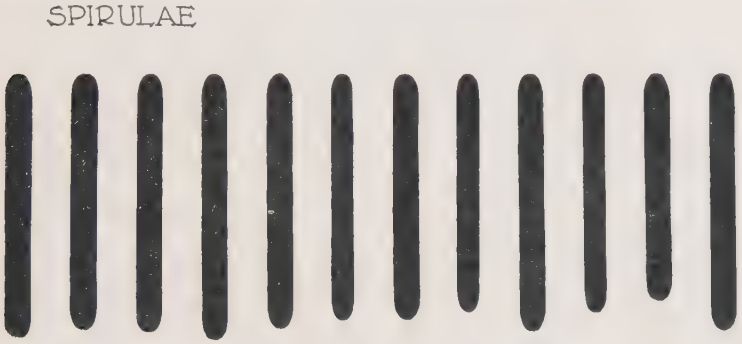
Text-Fig. 2.—Diagrams illustrating the average size of the capsules of the penicilli in the acontia of twelve specimens of *Sagartia elegans*. In this figure, and in Text-Figs. 3, 5–7, and 9–10, each diagram represents the average length and breadth of the capsules of a given type from a single tissue of a single individual anemone ; these figures are further explained in the text. A conventional shape has been adopted for all these diagrams, and all are drawn to the same scale ; they are not intended to illustrate the actual shapes of the various capsules, and they are slightly more approximate than the figures given in the tables at the end of the paper.

rosea, *roseoides*, and *miniata-ornata*), and the figures given are based on measurements of 30 capsules of each pattern from each specimen. These numbers are not large, but the measurements take a long time to make, and it is consequently impracticable to make them on a very extensive scale.

In the acontia of certain Actinians two types of nematocyst are plentiful. The first of these, a *penicillus*, is a capsule bearing a short, stout thread, barbed like a bottle-brush ; examples of this type are illustrated in Plate I, Figs. 5–7, and in Text-Fig. 1. In this type there is sometimes a slender terminal thread, which may be long or may be

short and wisp-like, at the end of the " bottle-brush " (as in Pl. I, Fig. 6, and in Text-Fig. 1, F) ; in other cases there is no terminal thread. The minor varieties within the type are characteristic of different species. The second type usually but not invariably possesses a smaller capsule, but a very much longer and more slender thread, the basal portion of which is either somewhat enlarged or bears well-developed barbs, or both ; this is known as a *spirula*, and is illustrated in Plate I, Figs. 2 and 3, and in Text-Fig. 1. Both of these types occur in *S. elegans*.

The figures for *S. elegans* are given in Table I on page 192 ; and in Text-Figs. 2 and 3 the average sizes of the capsules are represented graphically. From these figures it can readily be seen that the average



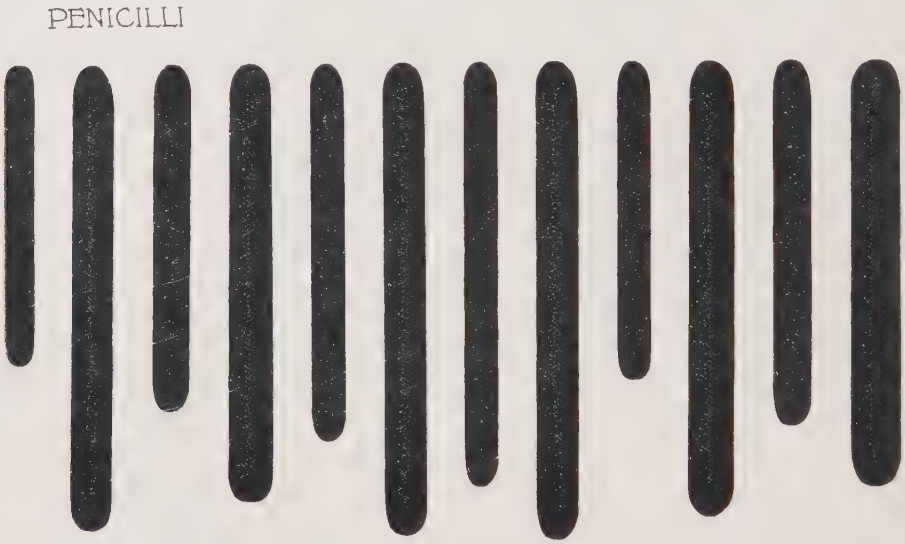
Text-Fig. 3.—Diagrams illustrating the average size of the spirulæ in the acontia of twelve specimens of *Sagartia elegans*—the same specimens as those from which the penicilli represented in Text-Fig. 2 were taken.

length of the capsule varies considerably from one specimen to another, but not within very wide limits. In these figures the diagrams are arranged in a graded series, so that the one representing the capsules of the largest specimen used is on the left, and that representing those of the smallest is on the right. From this it is evident that there is no strict relation between the size of the individual and the average size of its nematocysts. Text-Fig. 4 gives the maximum and minimum sizes of penicilli which were found in six of the twelve specimens, instead of the average.

B. Connection between the Size of the Animal and the Size of the Nematocysts.

The second point to be ascertained was how far, within a single stable species, the size of the nematocysts changes as the animal grows larger. It is impossible to tell the age of an anemone from its size, since size in these animals depends on the amount of food recently received, and not

upon age. But in a viviparous form one can at least distinguish new-born young from older individuals. The species chosen for this purpose was *Cereus pedunculatus*, and measurements were made from two new-born young and from 5 adult specimens forming a graded series from a small to a very large one. The acontia were used again here, and measurements were made from 30 examples of each of the two types of capsule contained therein. The figures are detailed in Table II on page 192, and the result is represented graphically in Text-Fig. 5, the diagrams being arranged in order of size of the specimens from which the capsules were taken; the diagram representing those of the largest



Text-Fig. 4.—Diagrams illustrating the maximum and minimum sizes of penicillus found in the acontia of six specimens of *Sagartia elegans*. The diagram on the extreme left refers to the same specimen as the one next to it; and so on, in pairs.

specimen is on the left. From this it will be seen that although the nematocysts of the new-born young are distinctly smaller than those of the adults of any size (and this was confirmed by further measurements from 4 other new-born young not detailed here), the size varies relatively little between the five adults, although these represent extremely different sizes of animal, No. 1 being many times the bulk of No. 5. Nor does the nematocyst-size increase regularly with the body-size.

C. The Nematocysts in the Acontia of the Species of Sagartia.

The third stage in the investigation was to find out in what manner nematocysts vary in a given tissue from one species of a genus to another.

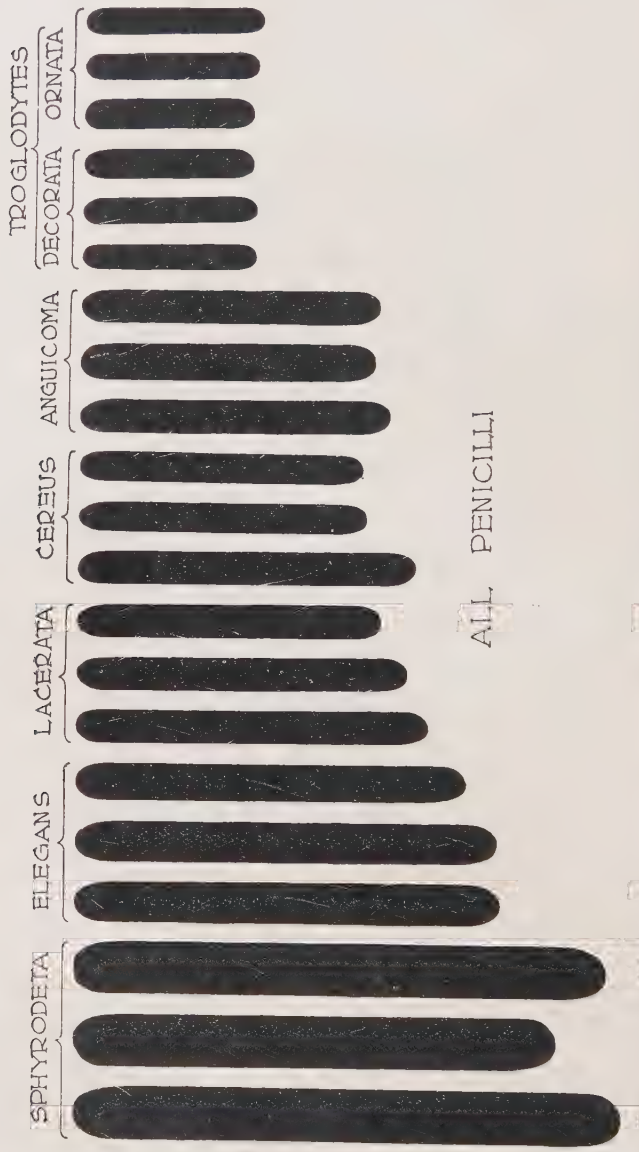
the genus Sagartia being used as a test-case. The acontia again were used, and nematocysts from three specimens of each Sagartian species were studied. By this time it had been realised that 20 measurements of any one type of capsule are enough to give a sufficient idea of the range

Text-Fig. 5.—Diagrams showing the average size of the penicilli and spirulæ in the acontia of seven specimens of *Cereus pedunculatus*. The diagrams are arranged in order of size of the anemone from which they were taken; that representing the capsules from the largest specimen is on the left. The two disgrams on the right represent capsules from new-born specimens.

of variation. In the measurements above recorded for *S. elegans* the average is very little different if calculated from the first 20 capsules measured, than if calculated from the whole 30. Consequently in the observations recorded from this point onward, the figures are taken from measurements of 20 specimens of each kind of capsule, except

in cases where for some special reason a smaller number only was practicable.

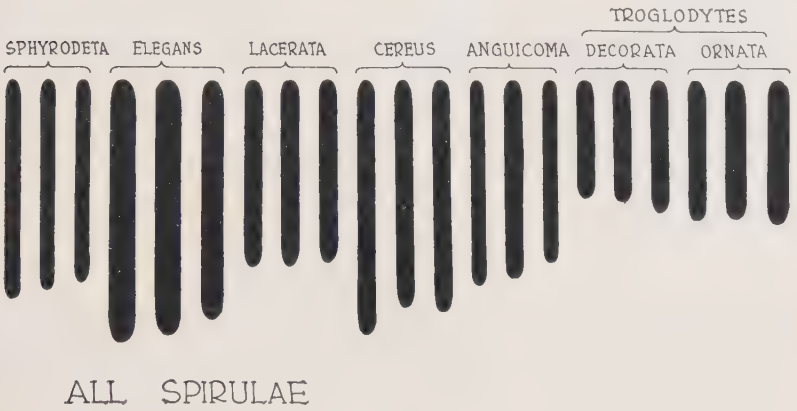
The figures relating to 4 species of Sagartia are recorded in Table III



Text-Fig. 6.—Diagrams illustrating variation in the average size of the penicilli in the acontia of five species of Sagartia (*S. sphyrodeta, S. elegans, S. lacerata, S. anguicoma,* and *S. troglodytes*) and of *Cereus pedunculatus.*

on page 193, and the average sizes of the capsules are indicated by diagrams in Text-Figs. 6 and 7 ; these latter include also *Sagartia elegans* and *Cereus pedunculatus* (which is very closely related to the Sagartias).

From Fig. 6 it will be clear that the penicilli of *Sagartia sphyrodeta* (a small species) outstrip those of all others in size, and that the penicilli of *S. troglodytes* (both varieties) are much the smallest. There would therefore be no difficulty in separating individuals of *S. troglodytes* from those of *S. sphyrodeta*, in a mixed collection, on the strength of these capsules; nor, indeed, would there be much difficulty in separating one of these species from any others, given well-grown specimens. If, however, one were to attempt the same feat with a mixed batch of *S. lacerata*. *S. anguicoma*, and Cereus, it would be quite another matter. These could, of course, be sorted out on other grounds; but from the



TEXT-FIG. 7.—Diagrams illustrating the average size of the spirulæ in the acontia of the same specimens as those from which the penicilli represented in Text-Fig. 6 were taken.

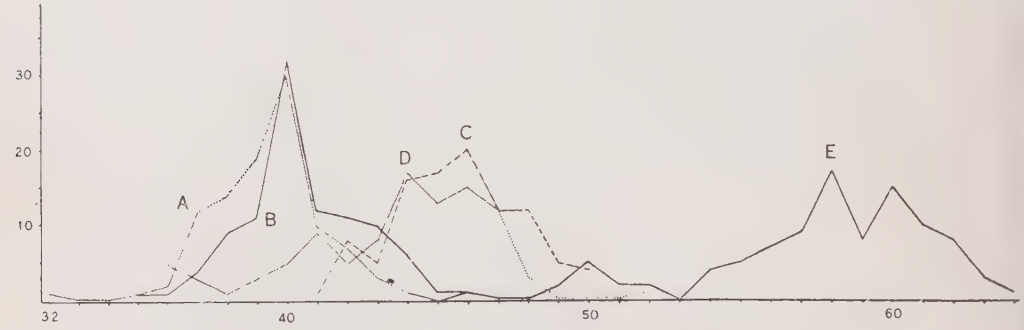
penicilli of their acontia they could not, since the range of variation in one would overlap the range in another, the size being distinctly similar in all. In order to make this still clearer, I made an additional series of measurements of the penicilli of a specimen of each of these species, and I measured also those of two specimens of *S. elegans*, measuring in this case 100 of each, so that curves might be drawn from the measurements. The result is shown in Text-Fig. 8, from which it may be seen that the curves for *C. pedunculatus* and *S. anguicoma* (extremely distinct species) are very similar; so are those for *S. lacerata* and a small specimen of *S. elegans*, which again are very different in other respects. In this particular figure the curves for *S. anguicoma*+*C. pedunculatus* are separated by a gap from those for *S. lacerata*+small *S. elegans*; but the gap between the small and the large *S. elegans* is greater. Moreover, it may be stated that by choosing one's specimens carefully these gaps could be filled in, and a graded series of curves produced, though the curves for the other species would hardly reach up to the level of the curve for the

large *S. elegans*, since this species does really tend to have larger penicilli than the others. But it must be evident from the contemplation of these curves that it would be quite unsafe to attempt to distinguish the species involved on the basis of the size of the penicilli of their acontia. Even if it be true that the capsules of each tend to occupy a given range of size, the ranges for the several species are very close to one another.

An important point which is demonstrated by the above table is that in all the species of Sagartia, as well as in Cereus, there are both penicilli and spirulæ in the acontia ; and the former are larger than the latter.

D. The Nematocysts in the Acontia of other Genera.

It was next desired to ascertain in what manner the nematocysts occur in the acontia of other genera of anemones which possess these organs, and this point was studied in as many forms as could be obtained alive.



Text-Fig. 8.—Curves illustrating variation in the length of the penicilli of the acontia in specimens of three species of Sagartia and in *Cereus pedunculatus*. Each curve is plotted from measurements of 100 capsules. The numbers along the abscissa represent the lengths of the capsules in μ ; those along the ordinate represent the number of capsules of each length (to the nearest whole number) in each 100 measured. A, *Sagartia anguicoma* ; B, *Cereus pedunculatus* ; C, *S. lacerata* ; D, *S. elegans* (small specimen) ; E, *S. elegans* (large specimen).

The result is detailed in Table IV on page 194, and in Text-Figs. 9 and 10. From these observations several facts emerge. The most important is that in the genera Phellia, Diadumene, and Aiptasia the acontia contain both penicilli and spirulæ in abundance, whereas in all the other genera spirulæ alone are present. No genus which I have studied possesses penicilli only. This confirms the idea which has been gained from other sources, that all the genera with spirulæ only are closely related, and that Diadumene and Aiptasia are more or less closely related to each other, but show less affinity to the other series of forms. As to Phellia, it is a genus of obscure standing, which I will deal with more fully in another paper. Another point which becomes clear is that in the genera with

spirulæ only (except Metridium) these are of very similar dimensions all the way through (see also Text-Fig. 9), and therefore their size is not of great value for purposes of identification.

The *details* of the nematocysts in these forms vary from one species to another—most distinctive are the large spirulæ of *Metridium senile*, which are unlike any other capsules I have seen. In these, the capsule itself is long, the thread is very long, and its specialised basal part, which is slender where it leaves the capsule, gradually widens to a maximum, then ceases abruptly ; this part is sometimes more than twice as long as the capsule. In the penicilli there is sometimes a slender terminal thread, which may be quite short, on the end of the " bottle-brush " portion (Aiptasia, Diadumene, *Sagartia sphyrodeta*), in other cases little or no trace of any such thread. Such differences, in some cases, are probably characteristic of species only ; in others they perhaps characterise genera.

E. The Nematocysts of Tissues other than Acontia.

Finally, a short study was made of nematocysts occurring in tissues other than acontia, and in anemones possessing no acontia. In the latter, special attention was paid to acrorhagi, which, like acontia, are special stinging-batteries. I should have liked to extend this section of the work much further than time allowed.

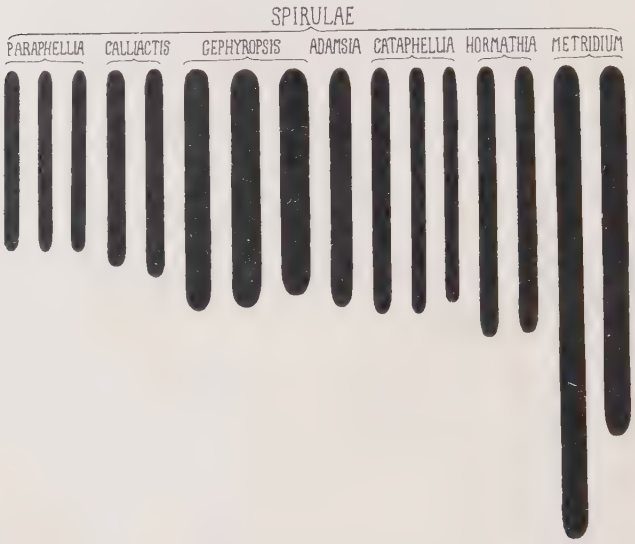
The tables relating to this section of the work (Tables V to VII) will be found on pages 195–197. The points which may be deduced from them are as follows :—

(1) In *Anthopleura ballii* and *A. thallia* the acrorhagi contain a special type of nematocyst not found, so far as I know, elsewhere in the body. To what type these capsules belong I am not certain, but I think that in *A. thallia*, at least, they may be spirocysts of a particular kind, and not nematocysts at all.

(2) *Bunodactis verrucosa* has the same nematocysts in the " acrorhagi " as in the rest of the body-wall ; the acrorhagi are therefore not special stinging-batteries in this case, but come under the heading of " pseudo-acrorhagi."

(3) In Peachia the prevalent nematocysts in the ectoderm of column-wall and tentacles, and the epithelium of the throat, are spirulæ of identical type, but of slightly different sizes. In the mesenterial filaments, however, there are three very distinct kinds of capsule ; one is a penicillus of a curious kind, one a large capsule of special type, with the basal part of the long thread very little differentiated (probably a modified spirula) ; the third an ordinary spirula. It is curious that the same general distribution of types occurs in the tissues of *Anthopleura ballii*, a form very different from Peachia.

(4) In *Phellia gausapata* both penicilli and spirulæ occur in the epithelium of column, tentacles, and throat, as well as in the acontia; those of the acontia are unlike the rest, and minor variations appear from one tissue to another.



Text-Fig. 9.—Diagrams illustrating the average size of the spirulæ in the acontia of anemones of several genera.

F. Other Data.

There has been discussion as to whether the capsule of a nematocyst is larger before explosion than afterwards. I have made a certain number of measurements on exploded and unexploded cysts of the same kind, from the same tissue and usually from the same sample; the results are given in Table VIII.

This table includes both spirulæ and penicilli, and these from more than one tissue. In all cases there is a diminution of volume after the explosion, although sometimes it is very slight. I have very few data to offer with regard to the effect of reagents on the size of the capsule. In a specimen of *Peachia triphylla* I measured a few capsules of each of the three types which occur in the mesenterial filaments, some in the fresh condition, others after fixation in formalin.

Type.	Average Size before Fixation.	Average Size after Fixation.
1.	$24{\cdot}8\times4{\cdot}2\ \mu$	$24{\cdot}8\times4{\cdot}0\ \mu$
2.	$46{\cdot}0\times5{\cdot}2\ \mu$	$46{\cdot}1\times5{\cdot}4\ \mu$
3.	$26{\cdot}5\times3{\cdot}9\ \mu$	$26{\cdot}0\times3{\cdot}7\ \mu$

In this instance, therefore, the fixation made no appreciable difference. I believe, however, that spirit affects the capsule more than formalin, and that nematocysts in sections are sometimes very considerably shrunken.

TEXT-FIG. 10.—Diagrams illustrating the average size of the penicilli and spirulæ in the acontia of *Phellia gausapata*, *Diadumene luciæ*, *D. cincta*, and *Aiptasia couchii*.

3. SUMMARY AND CONCLUSIONS.

The cnidæ or explosive capsules of the Actiniaria comprise two distinct kinds.

(1) *Spirocysts* (Pl. I, Figs. 1 and 4). Thin-walled capsules with a thread which is closed at the end, and which bears spirals but no barbs. They stain readily with acid fuchsin, but the capsular content does not stain. Found in the tentacles and peristome only, in most species; in other tissues exceptionally. The spiral bands on the thread swell up in sea-water, and on contact with foreign bodies spread out into a network of strands; the thread is therefore adhesive, and may not be poisonous. The thread, prior to evagination, is coiled in a neat spiral within the capsule.

(2) *Nematocysts* (Pl. I, Figs. 2, 3, 5–7, and Text-Fig. 1). Thick-walled capsules with a thread which is often open at the end and normally bears barbs. They typically stain with methylene blue, and the capsular content often becomes stained. Widely distributed in the tissues. Poisonous and penetrating. The thread, prior to evagination, may be variously arranged within the capsule.

The present paper deals particularly with the following points :—

(1) *Spirocysts.*

These have been very little studied here, because their distribution is limited, and as far as my experience goes they vary a good deal in size in the individual, and not greatly in character from genus to genus. The only suggestion I wish to make with regard to them is, that the ordinary and well-known type of spirocyst may not be the only kind in existence, and that there may be capsules intermediate in type between nematocysts and spirocysts. I suspect that the special capsules in the acrorhagi of certain species (e.g. *Anthopleura thallia*) may be spirocysts of an unusual kind, and I have seen in the ectoderm of the lower part of the body of *Sagartia anguicoma* and *S. troglodytes* enormous oval capsules of a peculiar sort. These have a thin collapsible wall, a stout and apparently unarmed thread which, before explosion, is coiled up spirocyst-wise within the capsule ; they stain with fuchsin (although less deeply than ordinary spirocysts), and I think they must be a form of spirocyst. Moreover, although I have not studied this point in detail, I think that nematocysts are more variable in their action towards methylene blue than is generally supposed.

(2) *Nematocysts.*

With regard to these capsules, it is evident that two general patterns of cyst are widely distributed among Actinians. These two types, the *penicillus* and the *spirula* (described on pp. 178–179, and figured in Pl. I, and Text-Fig. 1) are easily distinguished from one another, although each contains varieties ; and their distribution among the genera is of taxonomic importance. In one and the same tissue of an anemone there may be found spirulæ only, or both penicilli and spirulæ may be present together (possibly penicilli alone occur in certain cases). Furthermore, there may be present, for instance, two varieties of spirulæ as well as penicilli. Again, one or more of these kinds of capsule may be present in great quantity, others being more or less scarce (see note on p. 177). The following data refer to majority-forms only.

A. In the acontia of those Actiniaria studied which possess them, the nematocysts occur in two fashions ; in the first, the acontia contain

spirulæ only, in the second they contain both spirulæ and penicilli in abundance (i.e. there are 2 majority-forms of capsule).

B. Among the forms examined, the species belonging to a single genus have the same type or types of capsule in the acontia throughout, although the details may vary. Different genera, however, are in some cases sharply distinguished from one another by the nature of the nematocysts in their acontia ; in other cases this is not so.

C. In *Phellia gausapata*, a species containing both penicilli and spirulæ in its acontia, both of these types occur in other tissues as well. In Peachia and in *Anthopleura ballii*, the prevalent capsules are spirulæ throughout most of the tissues, but in the mesenterial filaments three types, including penicilli, occur.

D. The *size* of the nematocysts in the acontia is useful in some cases as a specific distinction. This applies to *Sagartia troglodytes* and *S. sphyrodeta*, which are separable from the other British Sagartias on the basis of the size of the penicilli in their acontia.

E. In other cases the size of the capsules in one species is so nearly similar to that in another, that no distinction of the two forms is possible on the basis of this character. This applies to the penicilli of *Sagartia anguicoma*, *S. lacerata*, *Cereus pedunculatus*, and in lesser degree to those of *S. elegans*.

F. The size of the nematocysts in the acontia is sometimes very uniform from one genus to another, and in such cases gives very little help for generic determinations. This applies to Adamsia, Calliactis, Gephyropsis, Paraphellia, Hormathia, and Cataphellia, a closely related series of forms, all possessing spirulæ only in their acontia.

G. The variation in size of the capsules within a species is indicated by an example in Text-Figs. 2–4.

H. The size of the animal has not very much effect on the size of the nematocysts, except in extreme cases (Text-Figs. 2, 3, 5, and Tables I and II).

The general conclusion which may be drawn from the above data is that the distribution of different types of capsule may be very important in dealing with generic (and perhaps family) distinctions ; and that the size of the capsule is useful as a *specific* character in certain cases, but useless in others. A good example of the ease with which genera are in some cases separable in this way is the case of Metridium and Diadumene. The young of *M. senile* and the adult of *D. cincta*, although perfectly distinct, are sufficiently similar in colour and facies to be confused with one another by an inexperienced observer. In the acontia of the Metridium, however, there are large spirulæ of a peculiar type, in abundance ; whereas in those of the Diadumene both spirulæ and penicilli

abound ; and it is not difficult to make a preparation which will reveal these facts.

It is therefore evident that, as in the case of every other character connected with Actinian morphology, the nematocysts provide valuable diagnostic features in some cases and not in others ; and this emphasises once more that in dealing with such animals the species cannot be understood unless the whole of the characteristics of the organism, and not a single series of features, be taken into account.

Carlgren has maintained for many years that no description of an Actinian is complete unless it includes details of the nematocysts, and that we cannot construct a final classification until we know enough about their occurrence in the group. He has provided measurements of the capsules in his own descriptions for some time. I am glad, as a result of the above study, to express my agreement with Carlgren in this matter, especially as I did not hold this view originally.

It is more difficult to deal with the nematocysts from preserved than from fresh material, because, although dissociated preparations can easily be made, one mostly sees the capsules unexploded or damaged, and it is not always possible to tell exactly to what type they may belong. As the *number of types present* is a factor often more important than the size, it is advisable to procure fresh material wherever possible.

In the various tables given on pages 192–198, the maximum and minimum dimensions which occurred among the capsules measured, as well as the average size, are stated. This gives a better idea of the situation than if one of these series of data only be quoted. Carlgren in his descriptions usually quotes the range ; personally I should prefer the average, since it is my impression that the majority of capsules are of sizes not very far from the average, and that although it is useful to know the maximum and minimum, these are less significant than the average.

The reason why acontia have been so much used in this paper is that it was thought probable that in these special stinging organs, if anywhere, differences of diagnostic value would appear. I think the result justifies this idea. Probably the state of affairs in the acontia gives a key to that in the rest of the tissues—if we may judge by *Phellia gausapata*.

Since the above work was finished, Carlgren has kindly sent me particulars of a similar study, not yet published, which he has made on Actinian acontia. He has observed as I did, that in Hormathia, Calliactis, Paraphellia, Adamsia, and Gephyropsis there are nematocysts of one type only in the acontia ; and to my list he adds the genera (mostly non-British) Actinauge, Phelliactis, Paracalliactis, Chondrophellia,

Allantactis, Cricophorus, Stephanauge, Acraspedanthus, and Phelliogeton. Carlgren finds also the two types of capsule in the acontia of Sagartia (including Thöe), Phellia, Cereus, Diadumene and Aiptasia (with allied forms), and adds to this list Artemidactis, Choriactis, Parathöe, Sagartiogeton, Andvakia, and Isophellia. Moreover, in two peculiar genera (Kadosactis and Sagartiomorphe) he has observed penicilli only in the acontia ; if these alone are present in quantity we have here a third type which I have not seen myself.

These investigations re-open the question of the classification of the anemones with acontia. I do not propose to discuss this subject in detail at present, but am willing to modify the scheme which I suggested in 1920, in the light of new knowledge. A provisional scheme which would meet with the views of both Carlgren and myself would be as follows.

1. Diadumenidæ, as defined by Carlgren, 1924, page 234. Acontia with both penicilli and spirulæ.
2. Aiptasiidæ, as defined by Carlgren, 1924, page 237. Acontia with both penicilli and spirulæ.
3. Metridiidæ. Including the Metridiidæ and Chondractiniidæ as defined by me in 1920, pages 526 and 533 (but omitting Sagartiomorphe and the Aiptasia group). For forms possessing spirulæ only, in the acontia ; base and basilar muscles ; mesenteries not divided into macro- and microcnemes ; usually six or about six pairs of perfect mesenteries. Cinclides present or not. Sphincter mesoglœal. Primary mesenteries often sterile.
4. Sagartiidæ. Including Sagartiidæ and Choriactidæ of my 1920 paper. The acontia possess both penicilli and spirulæ in abundance. Base and basilar muscles present ; mesenteries not divided into macro- and microcnemes, usually more than six pairs perfect. Cinclides present as a rule. Sphincter mesoglœal. Primary mesenteries typically fertile.
5. Carlgren suggests the possible addition to these of new families, Kadosactidæ (for Kadosactis and Sagartiomorphe) and Acraspedanthidæ (for Acraspedanthus and Phelliogeton). These forms I do not know personally, so cannot yet form an opinion.
6. Phelliidæ. I hope to deal with this family shortly, in a separate paper.
7. Forms with no base or basilar muscles must perhaps (certainly according to Carlgren) be classified separately. I will return to this later.

TABLE I.

Number, variety and locality of specimen.	Diameter of base of specimen used.	Type of Nematocyst.	Range of variation in size.	Average size.
1. venusta (Valencia)	2·1 cm.	Penicilli	48–56×5–6·5μ	53·3×5·1μ
		Spirulæ	30–36×2·6–4μ	32·5×3·1μ
2. venustoides (Plymouth)	1·6 cm.	Penicilli	40–57×4–6μ	51·6×4·9μ
		Spirulæ	29–35×2·6–3·5μ	31·6×2·9μ
3. roseoides (Valencia)	2·6 cm.	Penicilli	44–58×4–6μ	52·7×5·1μ
		Spirulæ	30–39×2·6–4μ	33·9×3·3μ
4. miniata (Plymouth)	2·8 cm.	Penicilli	40–62×4–6μ	55·9×5·3μ
		Spirulæ	31–38×3–4μ	34·3×3·5μ
5. venusta (Plymouth)	1·1 cm.	Penicilli	39–56×4–5·6μ	47·4×4·9μ
		Spirulæ	24–33×2·6–4μ	29·8×3·3μ
6. nivea (Plymouth)	2·1 cm.	Penicilli	42–60×4·6–6μ	55·4×5·4μ
		Spirulæ	26–38×3–4·5μ	33·7×3·7μ
7. rosea (Valencia)	2 cm.	Penicilli	50–58×5–6μ	54·4×5·5μ
		Spirulæ	29–36×3–4μ	32·7×3·5μ
8. nivea (Valencia)	2·7 cm.	Penicilli	50–62·6×4·6–6·5μ	57·1×5·5μ
		Spirulæ	28·6–37×3–4μ	34·0×3·4μ
9. miniata (Valencia)	1·0 cm.	Penicilli	45·2–59×4·6–6μ	53·6×5·1μ
		Spirulæ	31–38×3–4μ	33·9×3·4μ
10. venustoides (Valencia)	1·9 cm.	Penicilli	42–59×4–6μ	51·9×5·1μ
		Spirulæ	26–35×2·6–4μ	31·4×3·2μ
11. niveoides (Valencia)	2·6 cm.	Penicilli	46–58×5–6μ	54·1×5·4μ
		Spirulæ	28–37×3–4μ	33·5×3·5μ
12. miniata (Plymouth)	2·7 cm.	Penicilli	56–63×4·6–6·6μ	59·8×5·7μ
		Spirulæ	32–38×3–4μ	35·2×3·5μ

TABLE II.

Number of specimen.	Diameter of expanded tentacular crown.	Type of Nematocyst.	Range of variation in size.	Average size.
1	4·1 cm.	Penicilli	40–48·6×4–5μ	44·5×4·5μ
		Spirulæ	29–36×2·4–3·4μ	33·6×2·7μ
2	3·2 cm.	Penicilli	38–44×4–5μ	41·9×4·3μ
		Spirulæ	30–38×2·4–3·4μ	33·9×2·9μ
3	2 cm.	Penicilli	33–42×3·8–5·4μ	38·2×4·1μ
		Spirulæ	28–33×2·2–3μ	30·2×2·5μ
4	1·7 cm.	Penicilli	36–46×3·6–5μ	40·8×4·2μ
		Spirulæ	29–36×2·4–3μ	32·7×2·6μ
5	1·1 cm.	Penicilli	34–42×3·6–4·6μ	37·4×4·0μ
		Spirulæ	28–35×2–3μ	30·6×2·6μ

Number of specimen.	Diameter of expanded tentacular crown.	Type of Nematocyst.	Range of variation in size.	Average size.
6	·5 cm.	Penicilli	25·2–31·2×3·2–4μ	29·1×3·6μ
	(New born)	Spirulæ	25–30×2–2·6μ	27·1×2·3μ
7	·35 cm.	Penicilli	30–35×3·4–4μ	31·2×3·6μ
	(New born)	Spirulæ	23·2–29×2–2·4μ	26·5×2·2μ

TABLE III.

Species.	Number and locality of specimen.	Diameter of specimen.	Type of Nematocyst.	Range of size.	Average size.
Sagartia sphyrodeta	1	2·2 cm.	Penicilli	62–86×6–7·2μ	72·2×6·9μ
	Plymouth	(flower)	Spirulæ	24–32×1·6–2μ	28·6×1·8μ
	2	2·2 cm.	Penicilli	58–71·2×6·6–8μ	63·7×7·1μ
	Plymouth	(flower)	Spirulæ	24–29×1·6–2μ	27·4×1·8μ
	3	1·4 cm.	Penicilli	60–77×6–8μ	69·8×6·9μ
	Plymouth	(flower)	Spirulæ	24–29×1·6–2μ	26·7×1·9μ
S. anguicoma	1	4 cm.	Penicilli	38·6–43·2×4–5μ	41·1×4·6μ
	Plymouth	(base)	Spirulæ	23–31×2–2·6μ	27·0×2·2μ
	2	3·8 cm.	Penicilli	35–42×4–4·5μ	38·8×4·8μ
	Plymouth	(base)	Spirulæ	23–30×2–2·6μ	25·9×2·4μ
	3	2 cm.	Penicilli	34–44×4–4·6μ	39·5×4·4μ
	Plymouth	(base)	Spirulæ	19–26×2–2·6μ	23·9×2·2μ
S. troglodytes var. decorata	1	4 cm.	Penicilli	21–24×3·4–4μ	23·2×3·7μ
	Valencia	(base)	Spirulæ	13–17×2–2·6μ	15·3×2·4μ
	2	3·8 cm.	Penicilli	20–26×3·4–4μ	22·9×3·6μ
	Valencia	(base)	Spirulæ	14–17×2–2·6μ	15·8×2·3μ
	3	·9 cm.	Penicilli	20–25·4×3·2–4μ	22·7×3·8μ
	Torquay	(base)	Spirulæ	16–20×2·4–2·8μ	17·7×2·5μ
S. troglodytes var. ornata	1	·8 cm.	Penicilli	21·2–24×3·2–4·6μ	22·4×3·9μ
	Locality unknown	(base)	Spirulæ	17–21×2·2–2·6μ	18·5×2·5μ
	2	·9 cm.	Penicilli	21–25×3·4–4μ	23·1×3·6μ
	Millport	(base)	Spirulæ (unexploded)	16–20·6×2·6–3μ	18·7×2·8μ
	3	·9 cm.	Penicilli	21–26×3·2–3·8μ	23·6×3·5μ
	Locality unknown	(base)	Spirulæ (unexploded)	16 21×2·4–3·4μ	18·9×2·8μ
S. lacerata	1	1·8 cm.	Penicilli	41–51·2×4–5·4μ	46·7×4·6μ
	Plymouth	(base)	Spirulæ	22–27·2×2–2·6μ	24·4×2·4μ
	2	1·8 cm.	Penicilli	40–49×4–5μ	43·5×4·6μ
	Plymouth	(base)	Spirulæ	22–28×2–2·6μ	24·3×2·4μ
	3	1·2 cm.	Penicilli	38–44×4–5μ	40·2×4·4μ
	Plymouth	(base)	Spirulæ	23–26×2–2·6μ	24·0×2·3μ

TABLE IV.

Species and locality.	Number and size of specimen.	Type of Nematocyst.	Range of size.	Average size.
Paraphellia expansa (Plymouth)	1 2·8 cm. (base)	Spirulæ	22–26×2–2·6μ	24·2×2·2μ
	2 2·8 cm. (base)	Spirulæ	22–26×1·8–2μ	23·8×2·0μ
	3 slightly smaller than 1 and 2	Spirulæ	22–26×1·8–2·4μ	23·9×2·0μ
Cataphellia brodricii (Salcombe)	1 (base) 1·3 cm.	Spirulæ	30–35·2×2–2·6μ	32·5×2·3μ
	2 1·3 cm. (base)	Spirulæ	30–37×2–2·4μ	32·6×2·1μ
	3 ·9 cm. (base)	Spirulæ	27–36×2–2·6μ	31·1×2·1μ
Hormathia coronata (Plymouth)	1 2·25 cm. (column)	Spirulæ	33·6–37×2·6–3μ	35·6×2·7μ
	2 1·3 cm. (column)	Spirulæ	33–38×2·4–3μ	35·1×2·7μ
Gephyropsis dohrnii (Plymouth)	1 1·0 cm. (base)	Spirulæ	28–43×3·2–4μ	31·8×3·7μ
	2 1·0 cm. (base)	Spirulæ	28–34×3·8–4·6μ	31·5×4·1μ
	3 1·0 cm. (base)	Spirulæ	28–32×3·2–4μ	30·3×3·8μ
Adamsia palliata (Plymouth)	1 4·8 cm. (flower)	Spirulæ	28–35·2×2·4–3μ	31·7×2·8μ
Calliactis parasitica (Plymouth)	1 8·5 cm. (flower)	Spirulæ	24·6–29×2·4–2·8μ	27·4×2·6μ

Species and locality.	Number and size of specimen.	Type of Nematocyst.	Range of size.	Average size.
Metridium senile (Plymouth)	2 8·5 cm. (flower)	Spirulæ	24–28×2·4–2·6μ	26·1×2·5μ
	1 column 7 cm. high (adult)	Spirulæ	56–68×3–3·8μ	62·1×3·5μ
	2 base ·9 cm. across (young)	Spirulæ	45·2–52×2·6–3·8μ	48·4×3·4μ
Phellia gausapata (Wick)	1 large specimen	Penicilli	30–33×3–3·6μ	31·5×3·3μ
		Spirulæ	33–37×3·4–3·8μ	34·8×3·5μ
Diadumene luciæ (Plymouth)	1 ·5 cm. (base)	Penicilli	31–42·6×4·6–6μ	38·2×5·2μ
		Spirulæ (unexploded)	15–19×1·6–2·2μ	16·8×2·0μ
Diadumene cincta (Plymouth)	1 1·4 cm. (base)	Penicilli	44–52·6×5·4–7·4μ	48·3×6·1μ
		Spirulæ (unexploded)	15–18×1·4–2μ	16·4×1·7μ
Aiptasia couchii (Plymouth)	1 1 cm. (flower)	Penicilli	57–78×5·4–7·4μ	67·5×6·0μ
		Spirulæ	24–30×1·8–2·4μ	26·6×2·0μ
	2 1·3 cm. (column)	Penicilli	74–90×6–8·4μ	82·6×7·4μ
		Spirulæ	26–33×1·8–2μ	29·9×2·0μ

TABLE V.

Species with Acrorhagi, etc.

1. Anthopleura ballii, a Valencia specimen. Diameter of flower 4·5 cm. All capsules measured unexploded.

Tissue.	Type of capsule.	Range of size.	Average size.
Acrorhagi	Type 1. Form characteristic of the Acrorhagi	34–42·6×2·2–3μ	38·4×2·7μ
	Type 2 } Spirulæ	22–26×2–2·6μ	23·5×2·3μ
	Type 3 } Spirulæ	16–21×1·9–2·4μ	18·7×2·1μ
Ectoderm of column wall	Spirulæ	16–19×2–2·4μ	16·6×2·0μ
Ectoderm of tentacle	Spirulæ	22–27·2×2–2·6μ	24·5×2·4μ

Tissue.	Type of capsule.	Range of size.	Average size.
Mesenterial filament	Type 1. Penicilli	16·6–20×3·8–4·6μ	17·9×4·4μ
	Type 2. Large special kind	33·2–42×4–4·4μ	39·0×4·1μ
	Type 3. Spirulæ	16–17×2μ	16·7×2μ
Epithelium of throat	Spirulæ	28–31×2·6–3μ	29·2×2·9μ

2. Anthopleura thallia, a Torquay specimen. Height of animal 3·6 cm. Capsules measured unexploded.

Tissue.	Type of capsule.	Range of size.	Average size.
Acrorhagi	Type characteristic of Acrorhagi (Spirocysts also are present; so are Spirulæ)	36·6–45·6×4–5·4μ	40·6×4·7μ

3. Bunodactis gemmacea, a Plymouth specimen. Diameter of column 1·5 cm. Capsules measured unexploded.

Tissue.	Type of capsule.	Range of size.	Average size.
Pseudo-acrorhagi	Type 1. Rod-like kind	25–41·6×1–1·2μ	31·0×1·1μ
	Type 2. Spirulæ	11·2–14×1·6–2·2μ	12·8×1·9μ
Ectoderm of column wall	Type 1. Rod-like kind	25·2–38×1–1·2μ	32·3×1·0μ
	Type 2. Spirulæ	12–15×1·6–2μ	13·2×1·9μ

TABLE VI.

Peachia.

1. *Peachia hastata.* A Port Erin specimen. Total length (contracted) 2·2 cm. Capsules measured unexploded except in throat. Measured on one specimen except those of the tentacles, which were taken from another similar example.

Tissue.	Type of Nematocyst.	Range of size.	Average size.
Epithelium of throat	Spirulæ	21–25×2·6–3·6μ	22·7×3·2μ
Ectoderm of column wall	Spirulæ	13·2–16×2·6–3·4μ	14·8×2·8μ
Ectoderm of tentacles	Spirulæ	18–25·2×2·6–3·6μ	21·1×3μ
	Spirocysts	18–24×2·4–3μ	20·2×2·8μ
Mesenterial filaments (measured after fixation in formalin)	Type 1. Penicilli	16–18×3·8–4·6μ	16·9×4·1μ
	Type 2. Large kind	24–42×5·2–6·6μ	33·7×5·8μ
	Type 3. Spirulæ	20–27·2×3·4–4μ	24·2×3·7μ

Further measurements were made on 2 larger preserved specimens of *P. hastata* from Port Erin. I. Formalin specimen 5·6 cm. long. Filaments, Type 1, range 17–19·6×4μ, average 18·4×4μ; Type 2, range 26–41×4·6–7·4μ, average 31·4×5·4μ. II. Spirit specimen 6·5 cm. long. Filaments, Type 1, range 20–22×3–3·8μ, average 20·8×3·3μ.

2. *Peachia triphylla.* A Plymouth specimen. Total length (contracted) 4·1 cm. Capsules measured unexploded except in throat.

	Type of Nematocyst.	Range of size.	Average size.
Epithelium of throat	Spirulæ	24–28×3·4–5μ	26·0×4·1μ
Ectoderm of column wall	Spirulæ	15·6–19·6×2·2–3·4μ	17·7×2·6μ
Ectoderm of tentacles	Spirulæ	19–28×2·2–3·2μ	23·6×2·7μ
	Spirocysts	16–28×3–3·8μ	23·1×3·2μ
Mesenterial filaments	Type 1. Penicilli	23–27×4–4·6μ	24·8×4·2μ
	Type 2. Large kind	42–50×4–6μ	46·0×5·2μ
	Type 3. Spirulæ	24–28×3·8–4μ	26·5×3·9μ

TABLE VII

Phellia gausapata.

A large specimen from Wick, Caithness. Capsules measured unexploded except in acontia.

Tissue.	Type of Nematocyst.	Range of size.	Average size.
Acontia	Penicilli	30–33×3–3·6μ	31·5×3·3μ
	Spirulæ	33–37×3·4–3·8μ	34·8×3·5μ
Ectoderm of tentacles	Penicilli (commonest form)	14–18×3·2–4μ	16·4×3·5μ
	Spirulæ	16·6–21×2–2·4μ	19·7×2·1μ
	Spirocysts	14·6–29×2–4·6μ	22·9×3·3μ
Ectoderm of scapulus	Penicilli	16–18×3·6–4μ	16·9×3·7μ
Ectoderm of scapus (low down)	Penicilli	17 20×3·8–4μ	18·1×4μ
	Spirulæ	14–17·6×3·2–3·8μ	16·3×3·5μ
Epithelium of throat	Penicilli	21·2–25×3·8–4·6μ	23·5×4·1μ
	Spirulæ	24·6–29×2–2·6μ	26·8×2·2μ

TABLE VIII.

Species.	Tissue.	Type of capsule.	Average size before explosion.	Average size after explosion.
Paraphellia expansa	Acontia	Spirulæ	25·9×2·4μ	24·2×2·2μ
Cereus pedunculatus	Acontia	Penicilli	49·5×5·6μ	44·5×4·5μ
		Spirulæ	36·6×3·3μ	33·6×2·7μ
Peachia hastata	Epithelium of throat	Spirulæ	26·1×4μ	22·7×3·2μ
	Ectoderm of column wall	Spirulæ	14·8×2·8μ	14·0×2·4μ
Peachia triphylla	Epithelium of throat	Spirulæ	27·2×4·2μ	26·0×4·1μ
	Ectoderm of column wall	Spirulæ	17·7×2·6μ	16·4×2·5μ
Calliactis parasitica	Acontia	Spirulæ	29×2·9μ	27·4×2·6μ
Phellia gausapata	Ectoderm of tentacles	Penicilli	16·4×3·5μ	14·7×3·2μ
	Ectoderm of scapulus	Penicilli	16·9×3·7μ	14·8×3·2μ
Sagartia elegans	Acontia	Penicilli	67·2×6·9μ	59·8×5·7μ

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PLATE I.

Fig. 1.—A completely evaginated spirocyst from *Tealia felina*, very highly magnified. After Will, 1909a, Pl. 3, Fig. 4 (slightly modified). Here the spiral bands have partially disappeared, their substance having swelled and become drawn out into strands in places. Anastomosis has taken place between some of the strands.

Fig. 2.—An evaginated nematocyst (of the spirula type) from an acontium of *Sagartia elegans*. The long terminal part of the thread is not shown, and the barbs have fallen off, revealing clearly the spiral bands. The enlarged basal part is rendered wider than usual here by the medium employed (mercury medium; see text).

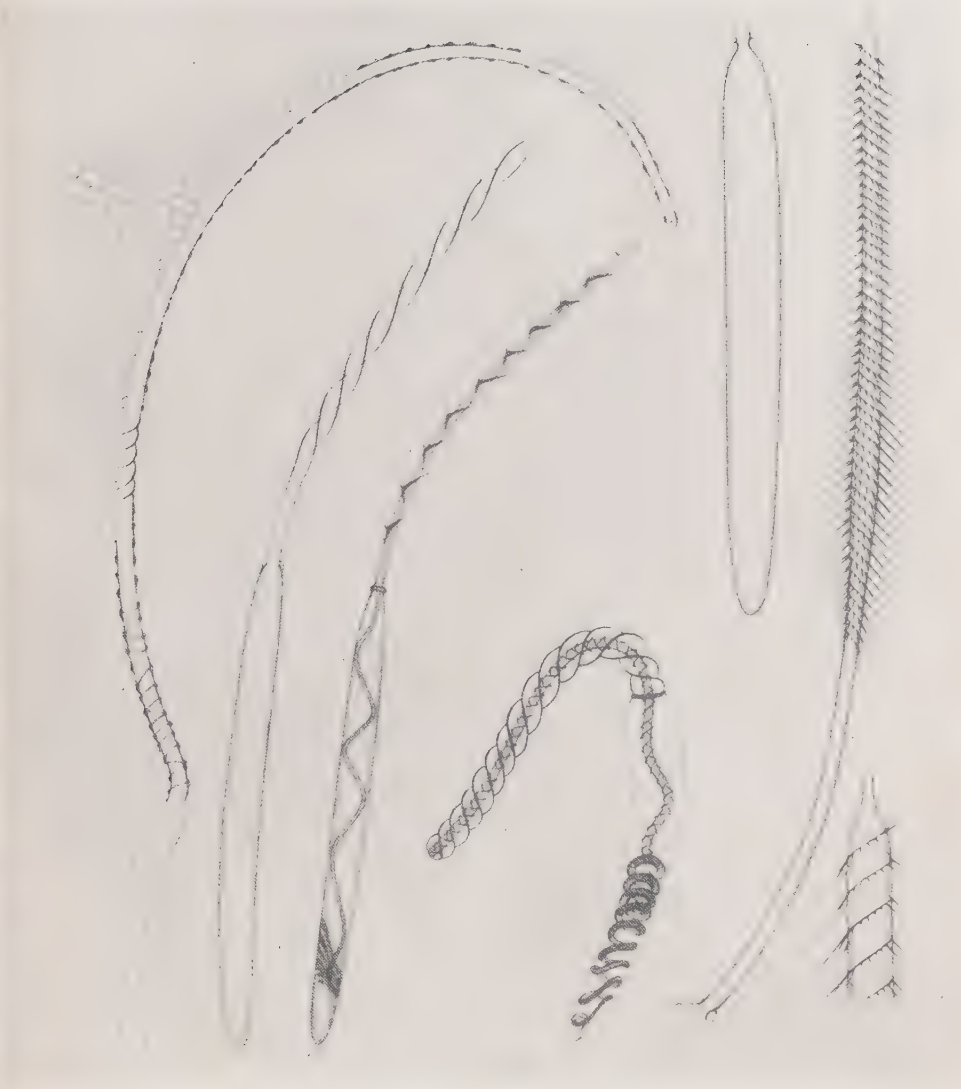
Fig. 3.—A partially evaginated nematocyst (spirula type) from an acontium of *Hormathia coronata*. The distal part of the thread is still inside the capsule. The individual barbs are not shown here, only the general effect produced; they are actually inserted in the manner shown in Fig. 7, but point the other way.

Fig. 4.—Spirocyst of *Tealia felina*, very highly magnified. After Will, 1909a, Pl. 3, Fig. 9. The thread is only partially evaginated. The spiral bands are clearly visible on the wide evaginated part; on the narrow portion which is not yet extruded the series of diagonal strokes represents the continuation of the spiral bands on the inner wall of this portion.

Fig. 5.—The capsule of an evaginated nematocyst (of the penicillus type) from an acontium of *Sagartia sphyrodeta*. Oc. 2, obj. 10.

Fig. 6.—The thread belonging to the capsule shown in Fig. 5, drawn to same scale. Slightly diagrammatic. The terminal portion of the thread is not shown, but was short and slender. The barbs were actually continued (though becoming more delicate) almost to the base of the thread, but were rendered barely visible in the lower part by the stain and medium employed (methylene blue used with potassium hydroxide and followed by mercury medium; see text). Oc. 2, obj. 10.

Fig. 7.—Diagrammatic enlargement of the terminal part of the thick region of the thread from another nematocyst similar to that shown in Fig. 6.



On a Fungus Allied to the Saprolegniaceæ found in the Pea-crab *Pinnotheres.*

By
D. Atkins, B.Sc.

With 13 Figures in the Text.

Introduction.

In the course of work on *Pinnotheres*, a fungus, which from its general characters would appear to be allied to the Saprolegniaceæ, was noticed in pea-crabs taken from mussels (*Mytilus edulis*) coming from beds in the estuary of the Camel near St. Issey Cliff (Padstow), from the estuary of the Yealm, and from near the junction of the Tamar and Tavy (Weir Point). Although the pea-crab lives in estuarine situations where the water is brackish, yet it may be taken in bivalves dredged in rather deep water on the coast (**1**, p. 123); those in the Laboratory were kept in the sea-water in ordinary circulation in the tanks and it was under these conditions that the fungus was seen to grow and produce reproductive elements. This fungus therefore attacks a marine invertebrate and, as far as I have been able to ascertain, it is the first member of the Saprolegniaceæ which has been so described. Some members of the family which occur on living freshwater fish are *Saprolegnia parasitica* Coker* on salmon, trout, etc.—stated by Patterson (**13**, p. 5) to be unable to grow in sea-water—*Achlya Hoferi* Harz on Bohemian mirror carp (**8**, p. 201; **2**, p. 145), *A. Nowickii* Raciborski on a sink carp (**2**, p. 147), and *A. polyandra* and *A. prolifera* on various fish (**9**, p. 108), while two which are found on freshwater plankton-crustaceans are *Leptolegnia caudata* de Bary on *Leptodora Kindtii* in Denmark (**14**, p. 511) and *Pythiopsis cymosa* de Bary on *Holopedium gibberum* in Lake Malmagen in Sweden (**14**, p. 511).

The mycelium of the *Pinnotheres* fungus may penetrate deeply into the body of the pea-crab, surrounding the organs, and may occasionally extend into the appendages, mouth parts, and even the eye-stalks, while it is generally found in the gills (Fig. 1). Such deep penetration of the tissue of the host would appear to be somewhat unusual among the Saprolegniaceæ, but it may also be effected by the salmon fungus where

* Coker (**2**, p. 58) considers that the fungus described from salmon and certain other fish as *Saprolegnia ferax* is distinct from that species, and he names it *S. parasitica*.

the way is prepared by *Bacillus salmonis pestis*, the bacteria breaking down the tissue which the fungus is then able to invade (**13**, p. 7), and by *A. Hoferi* of the Bohemian mirror carp, which is also probably preceded by bacteria (**2**, p. 145 ; **8**, p. 201). In these cases the fungus may penetrate the entire dermis with the exception of the muscles. The mycelium of *L. caudata* which attacks and kills *Leptodora* in large numbers, sometimes almost exterminating them from certain lakes in

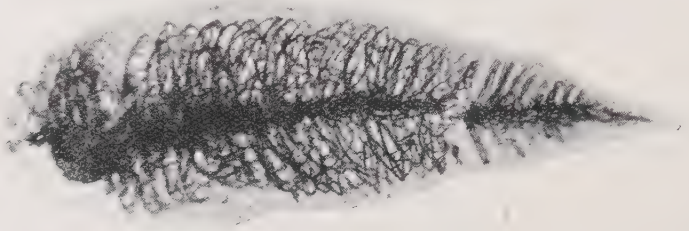


Fig. 1.—Photograph of a gill infested with the fungus, fixed in Flemming's fluid. × ca. 29.

Denmark, is said by P. E. Müller to envelop the organs. Petersen (**14**, p. 512) thinks that the mycelium usually enters round the mouth opening and, spreading rapidly, kills the animal, while it finally envelops both the mother individual and the eggs with a thick meshwork of hyphæ.

Description of the Fungus.

Mussels were obtained from Padstow on the following consecutive dates, November 25/27, February 24/28, April 25/28, August 1/28, and September 14/28, and a certain number of the pea-crabs taken from them on arrival at the Station either showed signs of the disease at the time or developed it later, but crabs obtained from mussels from the same place on October 11/28 were apparently free, for they did not develop it although many were kept together in bowls for about 6 weeks. Crabs which also developed the disease were obtained from near the junction of the Tamar and Tavy on March 22/28, April 10 and 20/28, and from the Yealm on July 21/28. The fungus would therefore seem to attack crabs during the greater part of the year in the comparatively mild climate of the south-west of England and is not restricted to the period of July to about the middle of September as are apparently the attacks of *Leptolegnia* on *Leptodora* in Denmark (**14**, p. 512). In some few instances it is certain that the crabs were already infected when taken from the mussels on arrival from the beds, and against the possibility of their acquiring the infection from the water circulating in the tanks in the Laboratory is the fact that crabs kept for over a year separately in mussels for rearing experiments have not developed the disease.

The presence of the fungus is mostly indicated some days before the death of the crab either by opaque white patches showing through the chitin of its body and abdomen, or else more rarely by the opaqueness of the gills, though a crab may die of the disease without any outward indication. The patches in the body generally occur over the gill chamber, especially the posterior region, though as the disease progresses the whole of the roof of the gill chamber may become involved. A white line is sometimes seen along the junction of the carapace with the

Fig. 2.—Broad, uncrowded hyphæ from roof of gill chamber. The protoplasmic contents are not shown, they were very finely granular with indication of vacuoles. × ca. 253.

This figure and all following ones were drawn from living material.

abdomen, and patches may also occur in the abdomen, where they are generally to be found round the junction of two segments. The white appearance due to the presence of the fungus can readily be distinguished from that due to parasitisation by a Sarcosporidian identified by Dr. Pixell Goodrich; in the latter case the muscles only become an opaque white. The white patches of the fungus probably surround the original point of infection, and from their position it will be realised that the fungus enters the crab either where the chitin is extremely thin or along the fine chitinous membrane which unites the segments of the abdomen, and the posterior border of the carapace to the abdomen. The white patches are

an intricately branched felt-like mycelium of fine hyphæ averaging about 9μ in width; occasionally very broad, uncrowded hyphæ up to about 32μ in width are found in the roof of the gill chamber (Fig. 2).

It appears that when the fungus enters through the exceedingly fine chitin roofing the gill chamber, it spreads for some distance in the tissue between it and the thicker chitin of the dorsal surface of the carapace, while it sends branches into the gills and sometimes the mouth parts. The fungus is most easily seen in these situations, but probably in some,

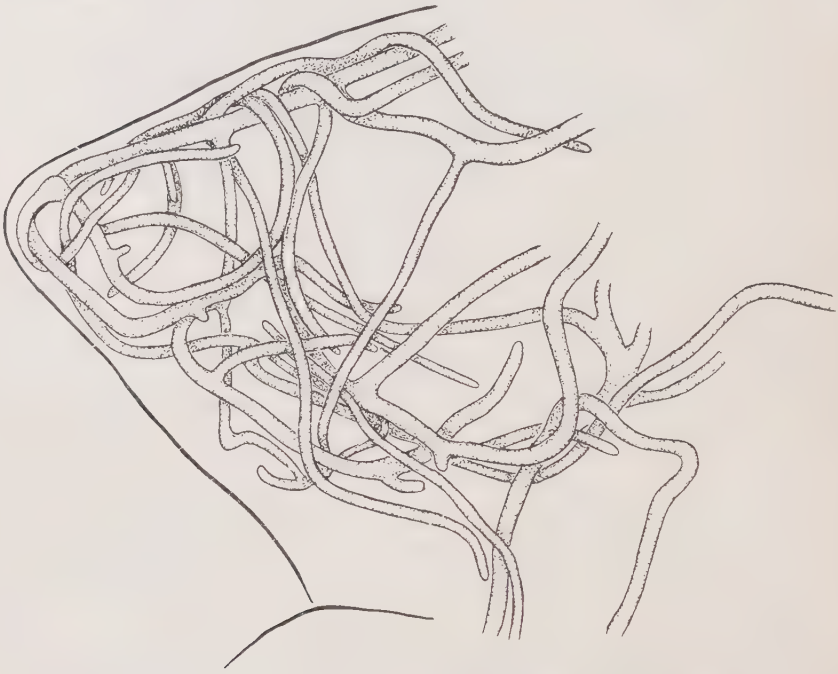


FIG. 3.—A rather heavy growth of the fungus in one of the larger leaflets near the base of a gill. × ca. 114.

if not all cases, it also extends into the body of the crab. Perhaps the easiest way of following the hyphæ, but only possible if the crab is small and thin-shelled, is to lift off the carapace, puncture the abdomen in several places, and fix the animal in Flemming's fluid. The oil globules, often present in great numbers in the hyphæ, are blackened by the osmic acid, and the branches of the fungus can be traced after clearing the crab in glycerine. By this means the fungus was seen without dissection in the body of three small crabs.

When the fungus has once entered the gills it soon absorbs the tissue and death of the pea-crab is rapid. It is an interesting possibility that in this case death may be due to asphyxiation.

In examining crabs for the presence of the fungus, when the white patches are absent, an inspection of the gills only has usually been relied on. A crab may die, however, when only one gill out of the six is infected, and therefore it would appear that in such a case there must be a considerable growth of the fungus in the body, unless laboratory conditions, which possibly included for these crabs shortage of food, markedly weakened them.

The fungus is most easily studied in the gills where the delicate chitinous

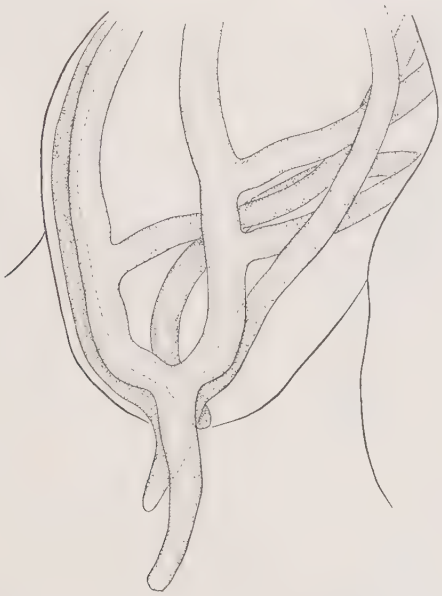


FIG. 4.—Sketch to show the very regular mode of growth of the hyphæ within the gill leaflet. The papillæ for discharging the spores are well developed but intact. The protoplasm is indicated by stippling, but no attempt has been made to show its structure. The thick lines show the outline of the gill leaflets. × ca. 253.

covering is so thin as to be transparent (Fig. 1). The hyphæ would seem to enter through the base of the gill from the infection area in the roof of the gill chamber and pass down the axis of the gill, giving off branches into the gill leaflets, both the axis and the leaflets soon becoming crowded with richly branched hyphæ (Fig. 3). At least in the young stages of the fungus the hyphæ keep within the leaflet, passing up one edge, curving very regularly round the tip, and passing down the other edge and so into the main axis, giving off branches on the way.

The whole of the contents of the hyphæ in the gills of the host gradually

divide into zoospores and no marked sporangia are formed. This fungus resembles *Aphanomyces* (**2**, p. 160) and *Leptolegnia* (**14**, p. 522) in that the sporangia are formed from unchanged hyphæ. Cross walls arise, but the portion cut off may be of considerable length with several branches; it may include a length running along the axis of the gill with loops into the gill leaflets, but apparently with only one exit. When the abdomen of

FIG. 5.—Sketch to show the fungus in three overlapping gill leaflets. Discharging papillæ are developing and show a bulge at the point of penetration of the chitin of the gill. The sketch was made at 8 p.m.; the next morning the filaments were empty, as was also the larger of the two reproductive bodies; the smaller, which had a wall dividing it from the hypha, was still full. The protoplasm is indicated by stippling, but no attempt has been made to show its structure, except in the two round reproductive bodies. The thick lines show the outline of the gill leaflets. × ca. 253.

the crab has areas of infection, hyphæ may pass into the pleopods and there become sporangia. A characteristic of this fungus is that the spore-producing filaments occur within the crab, though they would appear to be restricted to the gills and pleopods, the hyphæ in the roof of the gill chamber and in the body being purely vegetative. The reproductive hyphæ are generally stouter than the vegetative and are remarkably regular, tapering gradually to the tip with very clear and definite outline (Fig. 4). They vary in width from about 10μ to 20μ. Gills and pleopods

may be seen with a network of hyphæ empty except for a comparatively few spores which, unable to escape for some reason, have encysted there. The tissue of such gills and pleopods generally has disappeared entirely. It would seem that the filaments which enter these structures are entirely reproductive, though where infection takes place directly on the gill there is a tiny opaque patch of vegetative hyphæ. It may be that in the comparatively confined space of the gill or pleopod the tissue is soon consumed, and under these conditions spore formation naturally follows.

Fig. 6.—Sketches to show the development of a secondary discharging papilla when the tip of the first one has not given way. × ca. 342½.

Fig. 7.—Hypha growing up within an old sporangium after the *Saprolegnia* type of proliferation; it is much reduced in size where it penetrates the gill chitin. The tip of the hypha is of almost clear protoplasm. A few spores are lying free on the surface of the gill leaflet, the outline of which is shown by a thick line. × ca. 342½.

Klebs in 1899 showed that sporangia are formed only when the food-supply is quickly and markedly decreased (**15**, p. 484).

When spore formation is about to take place a small branch or papilla arises either from the end of a hypha (Figs. 7, 8A) or along its length (Figs. 4, 5, 9, 12) and the tip becomes applied to and penetrates the chitin. There is a slight bulging of the tip of the papilla, before the chitin is penetrated (Fig. 5). The branches to the exterior are mostly quite short, ranging between 0·03 mm. to 0·12 mm. It is by these short branches or papillæ that the zoospores pass to the exterior and, with very few exceptions, this is the only part of the fungus which extends into the sea-water. In one interesting case where the long blade-like exopodite of the second

pleopod of one side was infected, the long hairs were absent towards the tip, only their circular bases remaining, and the tips of the hyphæ were protruding through the centre of these cup-like bases. Branched discharging papillæ may occur where the tip of the original papilla has apparently failed to give way and a lateral branch has arisen through which discharge has taken place (Fig. 6).

Occasionally a new sporangium may grow up within an old one, as sometimes occurs in *Leptolegnia* (**2**, p. 157) and is typical in *Saprolegnia*, but the most that has been seen is one within another (Fig. 7).

The details of spore formation have not been observed. A gill which when pulled from a dead crab at night shows no sign of spore formation or of the discharging papillæ will the next morning be seen with a quantity of empty sporangia and with others in the process of discharging spores ; spore formation, however, occurs in gills in situ. Spore discharge seems most commonly to occur at night. The number of spores in a row in a sporangium varies with the width, from several to one or two.

The tip of the discharging papilla is mostly rounded ; it would seem to be forced off by the pressure of the zoospores packed behind it ; in one instance, however, the tip was flattened, with a fine membrane across it which appeared to dissolve. When the tip first gives way the zoospores pour out in a rapid stream, but when pressure is relieved they swim out singly ; once liberated, they swim off rapidly. Zoospores within the sporangia may be seen trying the various branches until they find the exit. If the exit should be blocked by an encysted spore, or if the sporangium is very long and branched, a considerable number of spores may be retained, becoming encysted.

The time during which the first zoospores may remain active varies considerably. They are apparently very susceptible to changes in the environment, for the placing of a cover-slip over a drop containing motile spores, just out of a sporangium, causes rapid encystment. Both within the sporangium and outside, zoospores may come to rest while still irregular in shape ; this is probably due to sudden change in the environment, such as increasing salinity on the slide. On the other hand, zoospores seen coming from a sporangium at 9.30 p.m. were taken up in a fine pipette and put on a cover-slip as a hanging drop ; many were still active 50 minutes later. The length of time during which the zoospores may remain active seems unusually long for the first zoospores, which in the Saprolegniaceæ apparently encyst after 5 to 15 minutes.

The first zoospores are of two sizes, large and small, as in *S. anisospora* de Bary (**2**, p. 33) ; the small are, however, comparatively rare. The small ones are about 8μ in length, the large about 14μ. Fig. 8 A and B shows sporangia from different parts of the same gill, one containing a few small zoospores, the other containing large ones ; the smaller appear to be more

regular in shape. Zoospores of intermediate size occur. The zoospores within the sporangia vary considerably in shape, especially in different sporangia. They may be oval, pear-shaped, or very elongated, almost rod-shaped, and may be rather irregular in outline, while some have a distinct protoplasmic tail. The zoospores appear capable of changing their shape to some extent, are slightly amœboid (Fig. 9). They are considerably flattened, as may be seen when they turn up an edge in swimming. It is probable that when free in the water they become a

Fig. 8,—A. Zoosporangium with small zoospores. In the lower right-hand corner are cysts formed from some of these spores within the sporangium. B. Zoosporangium with large zoospores. In the lower right-hand corner are cysts formed from some of the spores within the sporangium. × ca. 253.

more regular pear-shape. Zoospores swimming in the sporangia always keep the same end foremost, but in some cases the fore end is blunt, in others rather pointed, though generally all in the same sporangium swim with the same end foremost. The free zoospores have many shining droplets, and a small vacuole near the apex; they are biciliate but swim rapidly enough to make the number of the cilia and their attachment very difficult to discern. They move with the pointed end foremost and tend to swim in wide circles. The smaller zoospores, which seem to have a more regular shape, swim in a more straightforward manner and more rapidly. They often swing round in their tracks; this *volte-face* could be more easily understood if there were an anteriorly and a

posteriorly directed cilium. One apically attached cilium can be seen clearly, a second is sometimes glimpsed but is much more difficult to distinguish. A possible explanation is that this one, though also apically attached, is normally posteriorly directed and therefore often hidden by the body of the zoospore. In an attempt to make certain of the point of attachment of the cilia, zoospores were fixed in vapour of glacial acetic acid, then treated with iodine, but drops of sea-water containing the zoospores were also swarming with bacteria, which were particularly thick round the spores and often tended to arrange themselves on fixing, end to end in crinkled lines, sometimes touching the spores, so that any cilia were entirely hidden.

An interesting case was noted of spores emerging from a sporangium

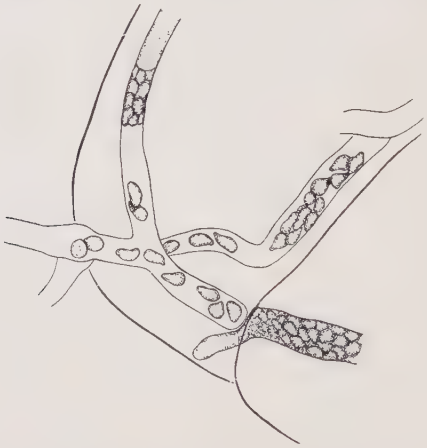


Fig. 9.—Sketch showing slightly amœboid zoospores within sporangia. A spore has encysted in the discharging papilla of one sporangium making it difficult for the zoospores to pass. × ca. 342½.

by way of a tiny discharging papilla which was markedly constricted where it penetrated the chitin of the gill. The emerging zoospores took a considerable time to pass through, they were almost pinched in half and detained there for perhaps 30 seconds. After passing through they halted at the exit for a few seconds as though held up by a posterior cilium or protoplasmic process adhering to the wall of the papilla; they would fling themselves sideways in an effort to become free.

As mentioned previously the length of time before encystment varies considerably, as does also the time taken actually to encyst. They may take several minutes in the process, swinging round and round in small circles and becoming more and more rounded until at last movement ceases; or a zoospore may stop abruptly when swimming rapidly, and,

as it were, tucking in the pointed end, become rounded in a second. When rounded the spore often swings round for a short time, and at least one cilium can be seen lashing. The spore comes to rest, a shining droplet appears on the tip of the cilium as it gradually shortens, and while still of some length it breaks off and floats away. This process of events was seen very clearly perhaps a dozen times and the path of the drifting cilium followed for a second or so. Generally only one cilium has been clearly seen during this process. The shortening of the cilia with the appearing of a droplet was noted by Butler in the encysting zoospores of *Pythium de Baryanum* Hesse (Pythiaceæ) (**6**, p. 94). On one occasion a zoospore of the *Pinnotheres* fungus, seen when about to encyst, had two

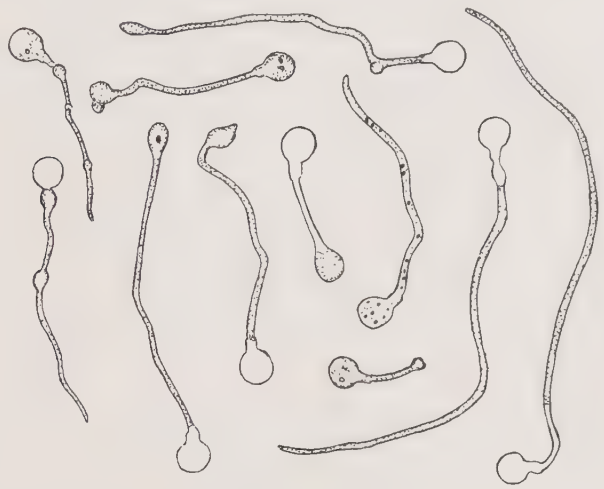


Fig. 10.—Germinating cysts. Some have small swellings along the length of the germ tube and one seems to be attempting to re-encyst. × ca. 685.

apical cilia which curled in towards each other, then broke off and floated away. The cysts vary from about 6μ to 10 or 11μ in diameter; they contain several shining globules. A fine germ tube is put out, but since no nutritive medium was supplied, as the tubes grew in length the part next the cysts was gradually left empty and after a time the plant died. Small swollen structures occur along the germ tube (Fig. 10), some nearly as large as the original cyst, as though there was an attempt at re-encystment (**3**, p. 283).

The question of the structure of the zoospores and as to whether there are two motile phases has had to be left, at least for the present, in a very unsatisfactory state. Owing to lack of time no attempt was made to obtain pure cultures and, as already mentioned, it was found impossible otherwise to obtain a drop containing zoospores that was not swarming

with bacteria, hiding the cilia. A second zoospore has not been observed emerging from a cyst, all that can be brought forward in favour of the existence of two motile phases in this fungus is, firstly, the finding of empty cyst cases with tiny exit tubes : the empty cases showed up quite clearly owing to the thick zone of bacteria collected round them. Secondly, the occurrence of a few zoospores of a definite bean-shape with two cilia which appeared to be laterally inserted, answering to the description of the second zoospores of the Saprolegniaceæ. These came from a sporangium, but may have emerged from spores encysted there.

Difficulty was experienced with growing the fungus in hanging drops of sea-water ; it was found that the development of the fungus in the

Fig. 11.—Young oogonium with applied antheridium (?). × 400.

Fig. 12.—Sketch to show part of a branched sporangium with a single aperture ; a number of zoospores have encysted within it. The thick line shows the outline of the gill leaflet. × ca. 253.

Fig. 13.—Sketch to show the highly vacuolated nature of the protoplasm in hyphæ which very occasionally grow out from the gill into the sea-water. × ca. 342½.

gills in such drops was arrested after a day or two, but that development would go forward and spores form if they were changed into a bowl of sea-water, even if growth had been at a standstill for 14 or so days. A somewhat similar state of affairs has been described by Lechmere (**11**, p. 318) for a species of *Saprolegnia*. The cysts formed in some of the hanging drops, probably owing to artificial conditions, did not develop and after a few days became enlarged, while their contents shrunk away from the wall, in some cases stretching in a band across the cell.

The infection and death was observed of a tiny nematode worm which had accidentally become fixed by its posterior extremity near the edge of a hanging drop made with an infected gill. The spores settled in the first place on the motionless tail of the worm ; the rest of the body was writhing vigorously for over 16 hours.

Sexual organs have not been definitely identified. Fig. 11 shows what

appears to be a young oogonium about 32μ in diameter with an applied antheridium of diclinous origin. In gills fixed in Flemming's fluid a very few round bodies containing many black globules of varying size have been seen. Similar bodies are shown in Fig. 5 which was sketched from fresh material. They appeared as shown at night, the next morning the larger one and the hyphæ were empty, the smaller still full. On two or three occasions two round bodies have been seen in proximity as in this figure. There is a possibility that they may be oogonia or gemmæ, but in any case they are exceedingly rare and are formed on spore-producing hyphæ.

Life-History (so far as known).

The mycelium enters the pea-crab in places where the chitin is extremely thin, and round the point of infection the hyphæ form a densely woven patch. In cases where the entrance is effected through the roof of the gill chamber, some strands pass into the body while hyphæ invade the gills and mouth parts. When the tissue of the gills is partly absorbed and the death of the crab is imminent, the hyphæ in these parts turn into zoosporangia, swarms of zoospores being liberated. These remain active under laboratory conditions for a period of a few up to at least 50 minutes, when they encyst. After encystment a second motile period may occur. Infection probably occurs during one or other of the motile phases. Organs which have been recognised as possibly sexual would appear to be rare.

Discussion of Relationships.

The *Pinnotheres* fungus has the general characters of the Saprolegniaceæ, the hyphæ, which are freely branched and unconstricted, are aseptate until the approach of the reproductive stages, and the asexual spores are biciliate. The zoosporangia are formed from unchanged hyphæ, as in *Aphanomyces* (**2**, p. 160) and *Leptolegnia* (**14**, p. 522); they are mostly branched (Fig. 12) as Coker (**2**, p. 159) observed for the sporangia in old cultures of *Leptolegnia* which may become very complex from the extension of a single sporangium into a number of adjoining branches. In both *Aphanomyces* and *Leptolegnia*, however, the spores are typically formed in a single row, while in the *Pinnotheres* fungus the number varies with the width of the sporangium. Very occasionally a second sporangium is formed within an empty one, a feeble development of the "nested" arrangement found in *Saprolegnia* and sometimes in *Leptolegnia* (**2**, pp. 22, 157). The biciliate zoospores on emerging from the sporangia swim actively away as in *Saprolegnia*, *Leptolegnia*, and *Isoachyla* (**2**, pp. 22, 157, 81; **6**, p. 83), and it is possible that after encystment a second zoospore emerges as also occurs in those genera. As previously mentioned, the first

zoospores are probably of two sizes, large and small, with intermediate sizes as in *S. anisospora* de Bary.

The *Pinnotheres* fungus is distinguished from species of Saprolegniaceæ growing on freshwater animals and apparently from all other members of the family (**6**, p. 82) by being almost entirely an internal parasite, the discharging papillæ of the sporangia only, with very rare exception, penetrating the chitin of the host and reaching the exterior. It is extremely rare for there to be any growth of the fungus, apart from the discharging papillæ, external to the host, but an exceedingly slight external growth was noticed on three occasions on gills. Such filaments are very different in appearance from the normal internal hyphæ from which they arise, they are very fine and exceedingly vacuolated, the squarish vacuoles stretching across the width of the hyphæ (Fig. 13). Similar very slender, highly vacuolated hyphæ were seen extending from a few well-developed embryos of *P. pisum ;* the hyphal threads radiating from the embryos had the appearance of a halo. These were found on August 21st and 12 days later the female, which was carrying the embryos, was found dead with white opaque patches on the abdomen and with the gills infested with the usual fungus.

Dead infected crabs, left in sea-water, show no external growth of the fungus and it seems probable that it dies soon after the crab. This is in striking contrast to the heavy external growth formed by *S. parasitica* on dead salmon and other fish, dead flies, beetles, etc. (**10**, pp. 321, 331), indeed this latter species is said by Patterson (**13**, p. 1) to show a richer growth on dead than on living salmon, indicating that dead tissue is much more suitable for its growth than the living fish. The apparent inability of the *Pinnotheres* fungus to form a growth on dead crabs may seem to argue in favour of its truly parasitic nature, but putrefaction of *Pinnotheres* is somewhat rapid and it may be that the number of bacteria, etc., present, check the growth of the fungus and kill it (**14**, p. 506 ; **10**, p. 331).

The question as to whether it is a true parasite or only invades tissue which has been broken down by parasitic bacteria, as does *S. parasitica* of the salmon (**13**, pp. 2, 7 ; **4**, p. 200 ; **7**, p. 29) and perhaps *A. Hoferi* of the Bohemian mirror carp (**2**, p. 145), has not been gone into : there is quite a possibility that this may be so, for gills infested with the fungus are almost always swarming with bacteria of several kinds. If it is a true parasite it would seem to be ill adapted to its host, for its penetration into the gills must soon cause the death of the host.

It is very probable that death occurs more rapidly under laboratory than under natural conditions. In the case of the crabs, of which details are given in Table I, they had been taken from mussels, being themselves parasites (**12**), and were isolated free in batches varying in number from

TABLE I.

MORTALITY OF PEA-CRABS, INFECTED WITH THE FUNGUS, WHEN KEPT TOGETHER IN BOWLS.

Number of crabs in a bowl, all of which died with the infection.	Date of placing in bowl.	Date of 1st and of last death.		Number of days before 1st death.	Number of days between 1st and last death.	Number of days between placing in bowl and last death.
5 (4 adult ♀+1 ♂) from Weir Point, April 10/28	April 10, 1928	April 28	May 18	18	20	38
12 (♀ adult) from Padstow, April 25/28	April 25	May 22	June 6	27	15	42
13 (♀ adult) from Padstow, April 25/28	April 27	May 12	May 25	15	13	28
7 (♀ adult) from Padstow, April 25/28	May 8	May 26	June 8	18	13	31
3 (♀ berried) from Padstow, April 25/28	May 8	June 4	June 13	27	9	36
7 (♀ adult) from Padstow, April 25/28	May 9	May 28	June 15	19	18	37
21 (♀ adult) from Padstow, April 25/28	May 10	May 22	June 11	12	20	32
18 (♀ adult) from Padstow, Sept. 14/28	September 17	October 6	October 20	19	14	33
				Average 19·4	Average 15·2	Average 34·6

5 to 21 in bowls of sea-water and therefore possibly able to obtain little food. When a number of crabs were kept together in a large glass dish, as in the eight instances given in Table I, they gradually died of the disease, one after the other succumbing. Mortality was very much lower among those crabs kept singly in finger bowls, indicating that the disease is extremely infectious. All crabs in the Laboratory had their water renewed every day or every other day.

The death of the host is generally sufficiently rapid, at least in the Laboratory, for the gonad—so far as appears outwardly—not to be affected. This is a condition contrary to that which occurs in infection by a Sarcosporidian identified by Dr. Pixell Goodrich, and in infection by *Pinnotherion vermiforme* Giard and Bonnier (**5**). In some few cases, mostly crabs which when taken from the mussels were seen to be infected, the crabs were rather orange or milky orange in colour. This possibly indicates that they may resist the fungus longer under natural conditions and there is time for them to draw on the gonad. In one dead crab examined, which had been a milky orange for some time, the fungal threads were found among degenerating ova in the gonad. The main axis of each of the gills was full of a bright yellowish orange substance, which looked like yolk globules, but did not blacken with the osmic acid in Flemming's fluid, and was doubtless derived from the degenerating ova.

SUMMARY.

A fungus, most probably allied to the Saprolegniaceæ, has been found infecting *Pinnotheres*. Pea-crabs so infected always die, but there is not as yet sufficient evidence to determine whether the fungus is pathogenic or only invades tissue which has been destroyed by parasitic bacteria. Although having the general characters of the family it apparently differs from all members so far described in that it occurs in a marine invertebrate and is almost entirely internal in habit, the zoosporangia occurring within the tissue of the host.

ACKNOWLEDGMENTS.

The work was carried out at Plymouth while holding a Miss Busk studentship of Bedford College. I wish to thank the College authorities for allowing me to work at the Marine Station, and the London University for granting me the use of their table. My thanks are also due to the Director and Staff for their kindness, and I am especially indebted to Dr. J. H. Orton for criticism and advice throughout the work. Miss G. L. Naylor most kindly read the manuscript. I am in addition indebted to several members of the Staff, and especially to Mr. A. J. Smith for the photograph in Fig. 1.

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The Larvæ of the British Sabellarians.

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With 9 Plates and 5 Figures in the Text.

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1. INTRODUCTION.

The larvæ of Sabellarians are some of the commonest of plankton organisms, and especially in the spring and summer months are present in abundance around our coasts. They have frequently been figured and described from plankton catches made in different parts of the world, but in nearly every case they have been regarded as larvæ of some form of Spionid, in spite of the fact that de Quatrefages (**18**) as long ago as 1848, Horst (**12**) in 1881, and von Drasche (**5**) in 1885 all obtained the early stages from artificial fertilisations of a species of Sabellaria. In 1914 Caullery (**3**), by comparing larvæ which he had caught in the plankton with the figures published by these three workers, and by calling attention to certain chætæ found in his oldest specimens was able to point out the

chief differences between the larvæ of Spionids and those of Sabellarians. In the same year Ziegler (21) again obtained the early stages of *Sabellaria spinulosa* by means of artificial fertilisations, but since then no further researches on these larvæ have been made. As yet no satisfactory account of the development of any Sabellarian exists, and the present paper gives for the first time a fairly full description of the development of the external features in two species of Sabellaria, and includes the first observations which have been made on the metamorphosis and early bottom stages of these remarkable creatures. All measurements are given in the legends to the text-figures or in the explanation of the plates.

It is a pleasant duty to have to thank Dr. Allen and the members of this Laboratory for their encouragement and help in this work. Dr. Lebour and Mr. A. J. Smith have both kindly attended to my plunger jars on occasions when I have been away.

2. METHODS.

In the early spring of 1927 a number of common and familiar larvæ were picked out from plankton catches and placed in bowls of sea-water. They were then thought to be Spionid larvæ, Caullery's paper not having been seen at that time. These larvæ after some weeks metamorphosed into what was, with some surprise, recognised to be the young of a species of Sabellaria. Two species of this genus are common in the Plymouth district, one, *S. alveolata* Linnæus forming large honeycomb masses of sandy tubes attached to the rocks on the shore at Whitsand Bay, the other, *S. spinulosa* Leuckart building separate sandy tubes attached to stones and shells on the bottom of the Sound, and elsewhere below low-water mark. Living specimens of both were collected, and artificial fertilisations made. Mature individuals of both species, and especially of the former, can be obtained during the greater part of the year, and they shed their genital products as soon as they are removed from their tubes. The early larval stages are easily obtained, and it is these which have previously been described by von Drasche and others. The early larvæ were placed in plunger jars or in finger bowls. The water used was obtained well out to sea, and was passed through a Berkefeld filter to remove any organisms it contained. A few drops of a culture of Nitzschia (kindly supplied by Dr. Allen) was added to each plunger jar or bowl, and this served as food. Numerous attempts to rear the larvæ in this manner were made, and some of these were successful. On the whole those in the plunger jars did best, but in several cases excellent results were obtained in the finger bowls. In warm weather those plunger jars which stood in an aquarium tank and were cooled and protected from rapid changes of temperature by running water gave the best results. It was also found important to

protect the jars from too strong a light, otherwise the diatoms became too numerous. The spines of the very young larvæ became attached to anything of a sticky nature, such as clumps of diatoms, and many larvæ often stuck to the same speck of debris, from which they were rarely able to free themselves. Older larvæ were powerful enough to pull themselves away. It is thus very important that the water should be perfectly clean. The water as a rule remained unchanged throughout each experiment.

There are two stages through which it is especially difficult to rear the larvæ. The first is the growth stage between the trochophore with nine or ten bristles in each bundle, and the considerably larger early metatrochophore with two or three trunk segments and a telotroch. Once that stage has been passed growth continues fairly readily until the larvæ are ready for metamorphosis. They then frequently die off, sometimes first making an abortive attempt to metamorphose. It was only after numerous attempts that artificially fertilised larvæ were reared to early bottom tube-building stages.

All the drawings, except where otherwise stated, are from living larvæ, confined in cavity slips but perfectly free to move about, so that the body was not distorted in any way. Proportions were obtained with the aid of a square-net micrometer in the eyepiece, drawing in the first place on to squared paper. Larvæ were also mounted in the usual manner for the better examination of the chætæ.

3. THE DEVELOPMENT OF *SABELLARIA ALVEOLATA* LINNÆUS.

(*a*) *The pelagic stages.*

When seen in the mass by reflected light, the freshly spawned ova of this species are purplish in hue. A conspicuous germinal vesicle is present and the eggs are very irregular in shape. If not fertilised, healthy ova will remain in this condition for several hours, but if sperm be added they round up and throw off a crumpled fertilisation membrane and the germinal vesicle disappears. After a time polar bodies are extruded and segmentation commences. Eighteen or twenty hours later the embryos show the first signs of movement. Fig. 1, Plate I, is a drawing of an embryo twenty-seven hours after fertilisation. The outline is rather irregular, and the embryo is densely granular and opaque. The colour is similar to that of the freshly spawned ova. It is surrounded by the crumpled fertilisation membrane through which cilia project. Just posterior to the equator there is a complete ring of very short fine cilia, the first sign of the prototroch. At the anterior pole a few very fine long cilia

form an apical tuft. The movements are rather feeble, but as the prototrochal cilia lengthen and become more powerful, the embryo begins to swim actively forwards, rotating on its longitudinal axis. The cilia of the apical tuft are usually directed forwards and twisted together. As the embryo develops its outline loses its irregularity, and, owing to a slight increase in size, it fills up the space inside the fertilisation membrane, smoothing out the wrinkles (Plate I, Fig. 2). This fertilisation membrane persists as the skin of the larva and is present up to the latest stage observed. It forms a rather close-fitting envelope separated from the "surface" of the larva by a narrow space. As this membrane is never tightly stretched, and as it is always of about the same thickness whatever the size of the larva may be, it is obvious that the original fertilisation membrane must be added to by secretion during growth. In only one culture out of many in which special attention was paid to this point, has the fertilisation membrane been observed to be actually thrown off. In this case, when a stage a little later than that shown in Fig. 2, Plate I, was reached, in many of the larvæ, but by no means in the majority, the membrane split right round in the line of the prototroch and was cast off in two pieces, one anteriorly and one posteriorly. This left the larva covered by a very delicate pellicle, and for two or three days it was possible, with a high power, to distinguish two kinds of larvæ in the bowl, those which had retained the membrane and those which had cast it off. Soon, however, it was no longer possible to do this ; all the larvæ had a typical membrane round them, which must mean that either those which cast it off had all died (many of both kinds of larvæ died), or had secreted another membrane indistinguishable from the true fertilisation membrane. In either event it is highly probable that the loss of the membrane was an exceptional occurrence.

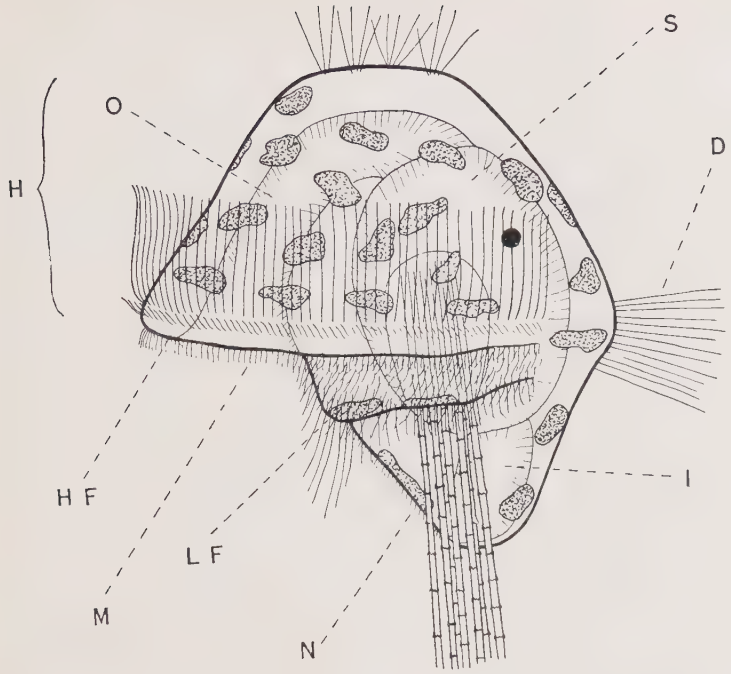
About forty-six hours after fertilisation the embryo reaches the stage shown in Fig. 2, Plate I. It is slightly elongated in an anterior posterior direction, and is opaque and granular in general appearance. With a high power the gut can be seen to be differentiating. The prototroch consists of a single row of fine cilia completely surrounding the body just behind the equator ; the long apical tuft is as in the previous stage, but at the posterior end a single extremely fine cilium, which persists for some considerable time (see figures), has appeared. A slight depression in the region of the future mouth deepens a little, and fifteen hours later is as shown in side view in Fig. 4, Plate I. By that time one long and one short provisional bristle have appeared on each side (Plate I, Fig. 3) and the general colour is an unevenly distributed yellowish green by transmitted light. Otherwise there has been little change. Shortly afterwards, however, the mouth appears as a small well-ciliated invagination situated just behind the prototroch in the slight ventral depression

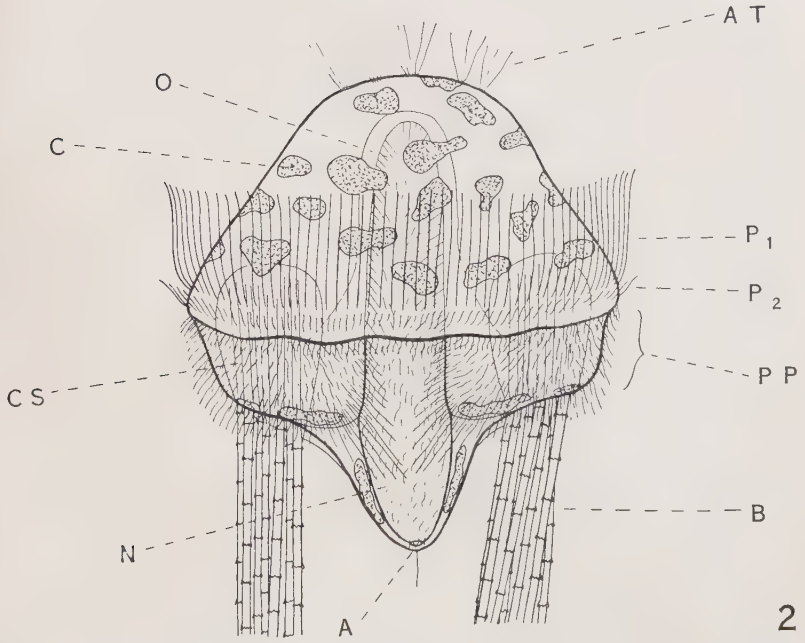
previously mentioned. About the same time the prototroch acquires a second and posterior row of very short cilia and becomes interrupted by a gap on the dorsal surface. First one and then another bristle appears in each bundle, and the yellowish green pigment, together with specks of brown, begin to be aggregated into chromatophores. The ventral depression deepens slightly, and the prototroch is raised up on a backwardly projecting fold which runs round the ventral surface just in front of the mouth and passes up on each side, but does not extend on to the dorsal surface. A neurotroch of short cilia appears on the ventral surface, and the forwardly directed œsophagus becomes ciliated and is a conspicuous feature of the ventral view. The apical tuft loses its longest cilia but persists as tufts of short fine cilia throughout pelagic life. Thus thirty hours after the last stage it reaches the condition shown in Figs. 5 and 6, Plate I. The larva is now much less granular and more transparent than previously, but there are still a great number of oily globules in the tissues.

About forty hours later, just over five and a half days after fertilisation, the larva reaches the stage shown in Fig. 7, Plate I. As this is the stage which has previously been specially figured by Horst, von Drasche, and Ziegler, and past which they failed to rear their larvæ, it is worth describing it in some detail. Text-Figs. 1 and 2 represent lateral and ventral views of a slightly older individual, but the only marked difference between it and the above-mentioned larva is that it possesses a few more bristles. Thus the following description, with that exception, applies to both.

The young Sabellarian has now reached what can be regarded as the fully developed Trochophore stage, and it has commenced to feed. The most striking feature is the backwardly projecting fold overhanging the mouth in front and passing round each side until it is lost as it merges into the dorsal surface. The whole of the region anterior to this fold can conveniently be referred to as the "hood." Behind this hood-fold there is on either side of the mouth a second rather similar fold or ridge which in later stages becomes more prominent. This structure will be called the "lip-fold." The diagrammatic section (Plate IX, Fig. 19) indicates the extent of the folding at this stage, while Text-Fig. 5, of the same but more highly developed structures in a larva which is probably that of Pallasia, gives a fair idea of the formation of this region in Sabellarian larvæ generally. The prototroch is carried near the edge of the hood-fold, it is complete ventrally but there is a large dorsal gap. It consists of an anterior row of long and rather strong driving cilia which form the chief swimming organ of the larva at this stage. Immediately behind a second row of shorter cilia occurs. In each of these rows the cilia are almost in single file, but as their points of attachment are not quite in line but are scattered a little, there is a slight tendency to form a very narrow band. Behind the second row there is a third line of short cilia along the edge of

the hood-fold and more cilia occur in the groove formed by the hood-fold, and also on the lip-folds. On the latter the cilia are usually grouped into two or three irregular bands running parallel with the edges of the folds. These cilia can be regarded as a posterior prototroch ; they are longest near the posterior edges of the lip-folds and especially at the posterior corners by the mouth. They probably form a food-collecting area, but attempts to prove this have been unsuccessful, largely on account of the minute size. The long cilia on the lip-fold corners are held more or less stiffly in the position figured and undergo vibratory movements. This distribution of the protrochal cilia is unaltered during the later pelagic stages, but in the drawings on the plates it has not been possible to indicate it very clearly owing to the relatively small size of the scale used. On the ventral surface between the mouth and the anus there is a rather deep wide groove, which is well ciliated by a broad neurotroch. The mouth leads into a ciliated œsophagus which runs forward, to open near the anterior end of the hood into a large globular stomach, also ciliated. A short ciliated intestine passes to the anus which is situated on the ventral surface close to the posterior end of the larva. On the anterior extremity of the hood, some tufts of fine apical cilia occur, while at the posterior extremity of the body a single fine cilium projects backwards. In the dorsal gap of the prototroch there is a prominent dorsal hump, and this carries a number of long fine but rather stiff cilia which occasionally vibrate. Four long provisional bristles (except in Text-Figs. 1 and 2, where there are more) project from a conspicuous chæta-sac situated on each side, and they pass out below the lip-folds. The chæta-sacs are moved by a series of muscles in such a way that they can direct the bristles in many directions. The structure of the bristles is very characteristic, they are surrounded by rings of teeth, the points of which are directed towards their distal extremities. Owing to the minute size and transparency it is extremely difficult, even with an oil-immersion, to make out the real nature of these rings. They appear to be collars arising from the bristle shaft with the free border of the collar toothed or serrated. The teeth are longer on one side of the collar than on the other (Plate IX, Fig. 11). The collars are arranged at intervals of about 8·5μ, but the distance apart varies. The larva is fairly transparent and has a considerable number of oily globules in its tissues. A conspicuous feature are the fairly numerous irregular chromatophores scattered over the hood (except on the anterior-dorsal region), on the dorsal hump, on the lip-folds, at the posterior end of the body, and one along each side just lateral to the ventral groove. The chromatophores have a fairly sharp irregular outline with a greenish yellow ground-colour, over which are scattered many irregular dark brown specks. One red eye-spot has appeared on the left side in front of the place where the prototroch stops short (out of sight in Fig. 7,





TEXT-FIGS. 1 and 2.—Lateral and ventral views of a trochophore larva of *Sabellaria alveolata* Linnæus. From life, slightly diagrammatic, ×624. Actual length (excluding bristles and apical cilia) approx. 100μ.

A, anus; AT, apical tufts of cilia; B, bristles, cut short; C, chromatophore; CS, chæta-sac; D, cilia on dorsal hump; H, hood; HF, edge of hood-fold; I, intestine; LF, edge of lip-fold; M, mouth; N, neurotroch; O, œsophagus; P_1, anterior or first row of prototroch; P_2, second row of prototroch; PP, posterior prototroch, or cilia on lip-folds; S, stomach.

Plate I). This and the eye-spots that develop later lie deeper in the tissues than do the chromatophores.

After the larva has reached the fully developed trochophore stage represented in Fig. 7, Plate I, no further differentiation of the soft tissues is apparent for some little time. The organism merely acquires more and more bristles until there are nine or ten in each bundle. During this period, which lasts for several days, sometimes about a week, the body of the larva remains the same size, or at most only becomes very slightly larger. At the end of the period it begins to grow and a constriction appears just in front of the chromatophores which are situated on each side of the ventral groove. The region behind this constriction becomes the telotrochal swelling (see p. 248 for reasons for using this term). At this period the telotroch is arising; the grasping-cilia (see p. 231) soon becoming quite prominent, but the driving cilia remain for some time fine, slender, and few in number. Meanwhile two more eye-spots have appeared, both on the right side. The second of these to develop arose posterior to and nearer the mid-dorsal line than the first. The fourth eye-spot does not develop until the larva has almost reached the stage shown in Fig. 10, Plate I, and it then appears posterior to and nearer the mid-dorsal line than the eye-spot on the left side, which was the first to appear. This curious order in the development of the eye-spots was constant in a large number of larvæ examined from different cultures, except that occasionally supernumerary ones might develop. Each eye-spot consists of numerous reddish globules (oily ?) aggregated into a cluster.

The larva drawn in Figs. 8 and 9, Plate I, was twenty days old, and it is definitely a metatrochophore. The telotrochal swelling and two or three trunk segments are marked out, but the limits of the segments are rather indistinct. The telotroch is present, but at this stage possesses a ventral gap, through which the neurotroch passes to the anus. There are three eye-spots, one on the left and two on the right side. Each bristle-bundle contains fifteen to seventeen bristles, one or two of them being quite short. In other details the creature closely resembles the trochophore, except that it is larger and the hood and lip-folds are more prominent. Growth continues and new trunk segments appear in front of the telotrochal swelling. A six-weeks'-old larva is shown in Figs. 10 and 11, Plate I, but many larvæ by this time are much more advanced. There is a great variation in the rate of growth of individual larvæ from the same culture, and reared in the same bowl or plunger jar. At the stage shown in these drawings, irregular pigment bands are present on the dorsal anterior part of some of the trunk segments, and they extend round the sides of the body to about as far as the borders of the wide ventral trough in which the neurotroch lies. These pigment bands ordinarily have a

black appearance, but they are really composed of a large number of very dark brown granules crowded together. Four red eye-spots are present in the positions indicated. The chromatophores have the same appearance as before, but they are confined to the hood, lips, dorsal hump, and the telotrochal swelling. On the hood they form a more or less regular line in front of the prototroch; elsewhere they are more scattered, but are absent from the anterior-dorsal area and from an area on each side just lateral to the eye-spots. The telotroch has either a ventral gap, or its cilia in that region are indistinguishable from the neurotrochal cilia which pass through it. In the ventral view the telotrochal swelling is represented as being turned slightly forwards; it is characterised by a number of clear vesicular-like "cells" that are present in addition to the chromatophores, which are rather darker than those on the hood. The larva is fairly transparent and very active.

Fig. 1, Plate II, shows in lateral view a larva from the same culture and plunger jar as the last, but only two days older. It was one of the more advanced larvæ referred to above. The trunk is much bigger in proportion to the hood than formerly. The three parathoracic segments are clearly defined, but as yet bear no parapodia. Behind them the first three abdominal segments have appeared; these bear slight lateral lobes, the first appearance of the dorsal uncinigerous processes of the parapodia. Between the parathoracic segments and the hood is a region more or less undifferentiated which will subsequently form into the two anterior thoracic segments of the adult. The most striking new feature, however, is the development of a pair of tentacles, one on each side of the dorsal hump at the place where the hood-fold edge merges into the dorsal surface. The attachment is almost in line with the end of the prototrochal row. These tentacles subsequently form the structures in the adult which are referred to as palps by many authors (e.g. Fauvel, **6**). Just ventral to each chæta-sac two small lobes have arisen, the largest of which will grow out into what may be called the ventral cirrus. The neurotroch is still a broad band of fine cilia, but cannot be seen in lateral view owing to the shallow trough in which it lies.

Another larva from the same culture, drawn seven days later, is shown in Fig. 2, Plate II. The dorsal parapodial lobes of the parathoracic segments have appeared, and each has two short bristles projecting from it. The uncinigerous lobes of the abdominal parapodia are larger, and now possess a number of uncini (Plate IX, Fig. 18); the first pair have four or five each, the second pair two each, and the third pair one each. The second pair of these uncinigerous lobes is situated more ventrally than the first and third pair. An important new feature is the appearance of a few special chætæ among the bases of the long provisional bristles. These chætæ will subsequently form some of the first crown

chætæ of the metamorphosed larva. Three kinds are present, one each of two sorts of bristles and a few paleæ of a curious broad flattened form (Plate IX, Figs. 13, 14, and 12). The tentacles are longer and are thickly ciliated on their ventral surfaces, but the cilia are not yet very active. They are not contractile (or very slightly so) and are held stiffly in the position shown. The cirrus ventral to the chæta-sac is quite long ; on it are a number of sensory cilia. The great chæta-sacs are passing backwards into a more posterior position. A horseshoe-shaped area around the posterior border of the mouth is becoming glandular ; it is the first appearance of the building organ. The ciliation is the same as described for younger larvæ except that there is no ventral gap in the telotroch. The driving cilia of the telotroch are longest at the dorsal ends of the row next to the grasping-cilia, and they gradually decrease in size and power as they approach the mid-ventral position.

The larva shown in Fig. 3, Plate II, was seven and a half weeks old, but was from another culture reared in the autumn of 1927, the larvæ of the previous drawings having been reared in the spring, but all died before this stage was reached. In its main features this larva is very similar to the preceding stage, but the body is more massive and the parapodia more distinct. Each dorsal bundle of the parathoracic parapodia consists of two prominent spear-headed bristles (Plate IX, Fig. 16) and two finer bristles (Plate IX, Fig. 17) which do not project much. In addition the third pair each has a long slender barbed bristle. Ventral bundles have also appeared on these segments, and have two fine bristles to a bundle. These cannot be seen in dorsal view, but are shown in Fig. 2, Plate III, which is a ventral view of a slightly later stage. The uncinigerous lobes of the first pair carry about ten uncini each, the second pair about five and the third pair about four. The numbers, however, vary considerably and need not be the same on either side. There are about thirty-five provisional bristles in each of the great bundles, and among them there are twelve to fourteen primary crown paleæ of the flattened type (Plate IX, Fig. 12) as well as the two short pointed bristles (Plate IX, Figs. 13 and 14) which were present in the previous stage. Owing to the greater growth of the body in comparison with the hood, the mouth and lip-folds are now well exposed. The building organ has increased in size, and the rudimentary parapodia of the two anterior thoracic segments are appearing. Fig. 2, Plate III, gives a good idea of the ventral surface of the anterior end, but in this drawing the structures are a little more advanced. There has been no change in the general ciliation except that the first signs of a nototroch are present on the first parathoracic segment. The tentacles are of considerable length, and are thickly ciliated ventrally. Chromatophores similar to those on the hood are present on their dorsal surfaces. The anus is situated on the apex of a slight cone. The

larva is rather opaque, the general body-colour being brownish. The chromatophores are darker brown than formerly, particularly those on the telotrochal swelling. The eye-spots have also become darker.

The larva has now reached the end of its pelagic development, but before describing the metamorphosis it will be well to consider the swimming movements.

(b) *Swimming movements and the "grasping-cilia."*

Sabellarian larvæ do not show a very active reaction towards light, but they do tend to keep on the side of the bowl or dish furthest from the window whenever the light is strong. This is most noticeable with the earlier stages after they have got one or more of their eye-spots. Polydora larvæ, under similar conditions, will be found on the side of the bowl nearest to the light (see Wilson, **20**, p. 577). They swim with the hood anterior to the direction of movement, and when watched in a plunger jar they will be seen, as a rule, to keep themselves orientated so that the hood is uppermost, i.e. in the position in which the figures are drawn. But they frequently depart from this upright position to swim in any direction, often moving along with the body placed horizontally. While swimming the two bundles of provisional bristles are kept close to the sides and the distal tips of the bundles meet one another above and behind the telotrochal swelling. The bristles pass through the dorsal gap in the telotroch and are held by the "grasping-cilia." The telotroch passes up the sides of the swelling on to the dorsal surface, and there the row of cilia turns abruptly forwards to form a longitudinal row on each side of a large dorsal gap. The cilia of these longitudinal rows project laterally and rather dorsally. They always remain more or less curved at their extremities, and although they undergo vibratory movements, they never actually beat. Their function is to curl round and grasp the long provisional bristles while the larva is swimming. Cilia with a similar function are present at the ends of the nototrochs—but not on the telotroch—of Polydora, and have already been described (Wilson, **20**, p. 577). In Sabellaria these cilia are much stronger and more conspicuous. Their function is probably twofold: (1) they help the larva's progress by holding in the bristles to the stream-line, and (2) their action must give increased rigidity to the larva as a whole and to the telotrochal swelling in particular, thus increasing the efficiency of the telotroch as a driving organ. In the later stages the driving cilia of the telotroch are longer and stronger than those of the prototroch, and possibly finally supersede the latter as a swimming organ. Under such circumstances anything which helps to make the soft body of the larva rigid will be to its advantage. The correctness of this interpretation appears to be supported by the appearance, during the later stages, of the single long barbed bristle from each

of the parapodia of the third parathoracic segments. These appear at a time when owing to the growth of the body the telotrochal swelling has been carried so far back that the grasping cilia can only just reach the tips of the provisional bristles. The two long bristles from the third parathoracic segment project further back than they do and are also held by the grasping-cilia. This will give rigidity to the body at a new point. In the latest stages, just before metamorphosis, it frequently happens that the long ringed bristles no longer reach as far back as the grasping-cilia unless the larva contracts its body. Fig. 3, Plate II, shows the body slightly contracted; it is frequently more stretched in the swimming larva, and then the grasping-cilia can only take hold of the barbed bristles from the third parathoracic segment. These bristles are lost during metamorphosis. It is interesting to recall the fact that in the development of the telotroch the grasping-cilia develop faster than the driving-cilia and are used for grasping the bristles while the latter are still fine and weak.

While swimming, a larva will every now and then suddenly flex the body ventrally so as to bring the telotrochal swelling close to the hood in the region of the mouth. At the same time the bristles are spread to point in all directions (Text-Fig. 3). This occurs when it bumps up against anything or is otherwise irritated. Tiny fishes have been seen to take larvæ into their mouths and immediately spit them out again with their spines erect. Some of these larvæ were afterwards examined; they appeared to be uninjured. This power of spreading the spines is acquired about the stage shown in Fig. 6, Plate I. The spines may also have a suspensory function, but this is difficult to prove. The larvæ frequently swim for long periods without erecting them and rarely have been seen to keep them spread for long, and then only while they were continually being irritated.

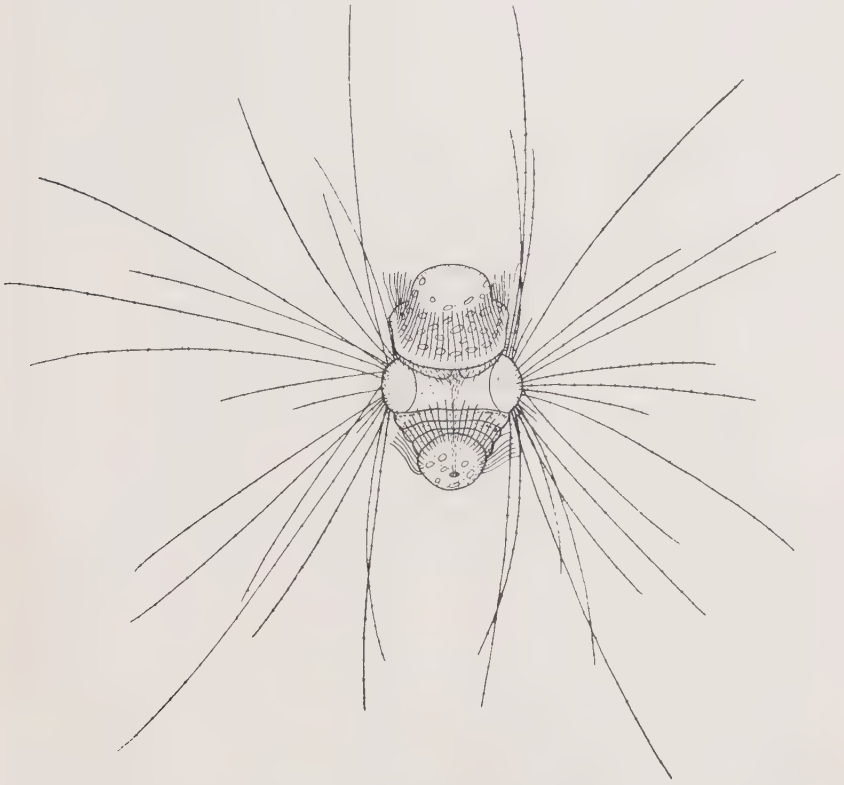
In all the figures, for the sake of clearness, the spines have been drawn in the partially erect condition. In Fig. 7, Plate V, the grasping-cilia are shown partially in action.

(c) *Metamorphosis and the early bottom stages.*

The duration of pelagic life varies within wide limits. Reared larvæ take from six weeks to three months from the time of fertilisation before they are ready to metamorphose. It is likely that the shorter period most nearly represents the time taken in the sea.

After a larva has reached the stage drawn in Fig. 3, Plate II, it shows an increasing tendency to crawl about on the bottom. This it does head downwards by applying the mouth to the substratum, on which the lips are spread out and flattened, the building organ being pushed back and stretched aside to allow of their full protrusion, so that their

ciliated surfaces, which are normally just inside the mouth opening, come into contact with the ground. The tentacles are turned outwards and forwards so that their ciliated surfaces also come into contact with the substratum. They are not, however, kept pressed against it, but are repeatedly raised up a little and put down again in a manner suggestive of feeling. In this way the larva glides forwards, the tentacles preceding and possibly testing the ground over which it travels. The hold is



Text-Fig. 3.—Ventral view of a formalin-preserved Sabellaria larva showing bristles erect. ×156. This is the position assumed when the larva is irritated and is characteristic of the larvæ as seen in preserved tow-nettings.

tenacious, a larva can resist quite strong squirts of water, and if it is clinging to the inside of a pipette is very difficult to dislodge. After crawling about for some time a larva may suddenly take to swimming again, settling down later on.

The change in habits is accompanied by changes in structure. The hood commences to shrink and the lips and mouth are exposed more and more fully (Plate III, Fig. 2). The building organ is enlarging rapidly,

and the first two thoracic segments begin to be defined by the growth of their parapodial rudiments. The body lengthens and the telotrochal swelling is flexed somewhat ventrally, while the cone bearing the anus grows out into a long process which turns forwards ventrally to form the characteristic caudal region of the adult. Ventral bristles appear on the abdominal segments and more nototrochs develop dorsally. Meanwhile great changes have been taking place in the head region. The hood has continued to shrink and the prototrochal cilia gradually disappear although some may persist for some time. The tentacles are in process of turning forwards permanently, and are becoming very contractile and wrinkled. In some cases a secondary tentacle is growing out on each side close to the anterior lateral corner of the mouth. These are probably the first filaments of what is sometimes called the palp (e.g. Benham, Camb. Nat. Hist., Vol. II). They are indicated as showing through the transparent tentacles in Fig. 1, Plate III, and are clearly shown, but are more highly developed in Plate IV. The great chæta-sacs have become fully exposed and have rotated a little so as to bring the ventral cirri into a lateral position. A second cirrus is present on the border of each chæta-sac close to the inner ventral corners. These secondary cirri were present as small swellings in the larva drawn in Fig. 3, Plate II, but they were then hidden between the bristle bundles and the back of the larva. The latter has now the appearance shown in Fig. 1, Plate III, and the long provisional bristles are rapidly falling out. The great chæta-sacs and the associated tissues turn upwards and forwards, at the same time shedding any provisional bristles which may remain. They finally take up a position projecting forwards and rather dorsally, and thus come to form the peduncular crown of the adult. These observations of the metamorphosis thus confirm the assumptions of descriptive morphologists that "les deux gros pédoncules operculaires représentent très probablement les rames dorsales fusionnées des deux premiers pièds rejetés en avant du prostomium" (Fauvel, **6**, p. 205).

The time taken to metamorphose varies, but appears to be normally about two days; it is often longer.

The specimen represented in ventral view in Plate IV was just over seven weeks old, and had probably metamorphosed a week or ten days previously. It was living in a little tube of mucus and debris on the bottom of the plunger jar. As this is, unfortunately, the most advanced stage to which the larvæ have been reared, it will be well to describe it in some detail. The peduncles project forwards and rather dorsally. On each twelve to fourteen primary crown paleæ (Plate IX, Fig. 12) are arranged in a circular row spread out fanwise from the centre. The circle is interrupted by a large gap on the side immediately facing the opposite peduncle. This is similar to the arrangement of the crown paleæ of the

adult. Inside the curve of the row and close to the gap are situated the two pointed bristles previously mentioned. These are shown in Figs. 13 and 14, Plate IX, the former being placed immediately lateral to the latter. Another pointed and curved bristle (Plate IX, Fig. 15) has appeared on the inner side of each peduncle below the level of the crown paleæ. The two cirri are prominent and probably represent the first of the numerous papillæ which in the adult form a row just below and outside the outer row of crown chætæ. In a median position, just ventral to the gap between the peduncles, is a strongly ciliated conical process, formed in front of the eye-spots during the shrinkage of the hood. The four eye-spots are still present, but the anterior pair (indicated in Plate IV) are closer together than in the larva. The eye-spots are almost black with a reddish tinge. The tentacles project forwards and outwards; they are strongly wrinkled and contractile, and have thickly ciliated ventral surfaces. Along their edges there is on every wrinkle a pair of specially stout cilia, and there are a number of these cilia on the tip. Just ventral to their place of attachment a dark brown swelling represents the remains of the hood. The brown pigment is a concentration of the brown specks of the chromatophores, the latter having shared in the general shrinkage of the hood. The prototroch disappeared long ago. The lip-folds form prominent ciliated lateral lips. Close to the anterior lateral corners of the mouth are a pair of wrinkled "tentacles" ciliated on their anterior surfaces in a similar way to that in which the ventral surfaces of the tentacles are ciliated. These "tentacles" are probably the first of the many filiform tentacles, sometimes referred to as the palps (Benham, *loc. cit.*), which are such a conspicuous feature of the ventral region of the head in the adult. Posterior to the mouth is the large glandular horse-shoe-shaped building organ. This is finely ciliated, especially on its anterior border and in the deep groove between it and the lateral lips. At each anterior lateral corner of this structure is a short process with sensory cilia and two fine capillary bristles, the rudimentary parapodia of the first thoracic segment. A short distance behind these a second similar pair of projections with one fine capillary bristle each represent the second thoracic segment. Then follow the three parathoracic segments with four bristles, two prominent and two inconspicuous (Plate IX, Figs. 16 and 17) in each dorsal bundle, and with two fine capillary bristles in each ventral bundle. The first three pairs of uncinigerous dorsal processes are prominent. The first pair are considerably broader in a dorso-ventral direction than the posterior two pairs, and they have about ten to twelve uncini (Plate IX, Fig. 18) each. The second pair possess five or six uncini each and the third pair four or five. The numbers of uncini vary considerably. In the drawing the ligaments attached to the uncini are indicated. Ventral to each uncinigerous

process is a single long fine bristle representing the ventral bundle of the parapodium. Behind the third pair of processes two slight swellings will probably develop into the fourth pair. Posteriorly the body curves forwards ventrally and is continued as the caudal appendage, on the extremity of which the anus opens. Close to the base of the caudal appendage and on the inner surface of the bend there is a small swelling which contains a mass of dark brown pigment. This is the shrunken remains of the telotrochal swelling.

A certain amount of black pigment—really composed of dark brown granules—still remains, especially on the dorsal surface. The worm on the whole is rather opaque, and the segment limits, particularly those of the abdominal segments, are not very visible. Nototrochs are present close to the posterior borders of the segments, and also on the head, the arrangement being the same as that shown for a more advanced individual of *S. spinulosa* in Fig. 1, Plate VIII. There is also a neurotroch in a shallow ventral groove.

The gut is divided into several regions. In the parathoracic segments the rather thick wall contains a fair number of small oily globules. On either side is a large gland, probably the thoracic gland shown in the figure of a young individual in McIntosh (**16**), p. 28, Fig. 139. A clear portion with only very few small globules in the walls follows, and this portion close to the posterior end of the first abdominal segment leads into a part where the walls are crowded with many closely packed large oily globules, in which condition the gut continues to the anus. This latter portion is indicated in Plate IV. It is a very conspicuous feature of the young worm and indeed of the later larval stages where it is situated further forward and may be present as early as the larva shown in Fig. 10, Plate I. This characteristic appearance has been omitted in the earlier drawings for the sake of clearness.

During the later stages much individual variation respecting the relative times of appearance of the different organs occurs. This is well seen in the development of the caudal appendage, for while in some individuals (as in Fig. 1, Plate III) it is quite large before the crown paleæ have been directed forwards, in others it does not develop until some time after the head region has fully metamorphosed. In such cases the telotroch persists although the worm is living in a tube. Again, the palps or tentacular filaments at the anterior lateral corners of the mouth in some cases appear quite early (as in Fig. 1, Plate III), in others very much later. All grades of intermediate conditions are found. Other organs show similar variation, although perhaps in lesser degree.

(d) *The building of the first sandy tube.*

The young worms after metamorphosis were frequently, but by no means always, found to be living in tubes of mucus on the bottom of the bowl or plunger jar in which they had been reared. To the sides of these tubes debris of various sorts was attached, especially masses of living diatoms and the cast-off provisional bristles. The tubes could be detached with a pipette and then if the larvæ were supplied with fine sand they would readily build in dishes or cavity-slips, while being watched through the microscope. All larvæ with mucus tubes were able to build tubes of sand grains, the mucus tube forming a foundation. All larvæ which were without mucus tubes, either because they had been removed from them or because, apparently, they had not made them, were unable to construct sandy tubes. They would attempt to do so, but they only succeeded in cementing grains into an irregular mass, even though they were kept amid sand for several days and in some cases were supplied with pieces of sterilised oyster shell—plentifully sprinkled with sand—which might serve as an irregularly creviced substratum on which to build. Some larvæ which metamorphosed in a dish containing sand also failed to construct either a mucus or a sandy tube. The explanation of this is not apparent.

To return to the worms with mucus tubes. As soon as sand grains are supplied, some are seized by the tentacles and conveyed to the mouth. The ciliated ventral surface of a tentacle is applied to a grain and immediately it is caused to travel towards the base. The grain is moved along by the cilia, on which it appears to be balanced or held, and it probably does not come into direct contact with the surface epithelium at all. The special strong cilia arranged in pairs along each side of the tentacle appear to play an important rôle in transporting particles. A grain is not seized by a tentacle curling round it, indeed the tentacles are never sharply bent. If the worm be lying back downwards in its tube (which in these observed instances was always horizontal) the tip of a tentacle will be inserted under a particle which will then travel along with its weight supported by the cilia. This is illustrated in Fig. 2, Plate VIII. If, on the other hand, the worm be lying back upwards the tip of the tentacle will be placed on top of the particle and it will slide over the substratum. It is uncertain as to whether one tentacle alone can actually lift a particle, but the two together applied on either side can do so and are sometimes so employed, if the particle be a big one. The "palps," if long enough, also assist in the collection of building material. In one of these ways grains arrive one at a time, to be held in the mouth by the lips. The first few are cemented round the edge of the mucus tube and then others are cemented to them. While holding a grain in its mouth,

the worm moves backwards in its tube so as to bring it into contact with the tube edge. It then moves forwards a little and turns the grain slightly, and then moves back once more. This backward and forward motion continues for a time, the worm continually twisting and turning the grain, trying it in different positions and at different places on the tube edge. If finally the grain more or less fits, possibly if it jams a little among those already fixed, it is cemented into place. But if after a few attempts it does not fit, it is discarded and another tried. Some worms will in this way discard several grains for every one fitted, others are more persistent in trying each particle. One larva in particular discarded very few grains; it would try each again and again all round the tube edge, turning it between every attempt, so that nearly every particle tried was finally fitted in somewhere. A particle appears to be cemented into position by the building organ, which is passed a few times over the place of contact on the inside of the tube. This rubbing of the building organ over the place of contact was seen every time a particle was fixed. Possibly the latter is also coated with some sort of cement while it is being turned about in the mouth. Fig. 2, Plate VIII, is a drawing of an actual tube. The mucus tube is covered with irregular clusters of diatoms and other debris, among which some of the larval provisional bristles are visible. The worm is shown in the act of collecting sand grains with its tentacles and one grain is held in the mouth.

The sandy tube is usually built rather slowly, the worm taking frequent rests. In one case, about thirty grains were fitted in four and a half hours, and by the next day the tube was more than twice as long. In another case—that of the particularly persistent larva mentioned above—a tube of about forty-five sand grains was constructed in two hours, while another individual during the same time fitted about thirty grains. The last tube was roughly as long as the body of the worm excluding the tentacles. On the whole, the building operation impresses the observer as a rather clumsy proceeding; certain operations are performed more or less persistently, and it appears to be a mere matter of chance as to whether any particular particle is fitted or not.

4. THE DEVELOPMENT OF *SABELLARIA SPINULOSA* LEUCKART.

(a) *The pelagic stages.*

The development of this species follows so very closely in almost all its details the development of the preceding species that a separate full description is unnecessary. Only those points, therefore, in which it differs in any way from *S. alveolata* will be dealt with in this account.

The drawings (Plates V to VIII) will serve as a further source of information.

The ova of *S. spinulosa* are on the whole slightly smaller than those of *S. alveolata*. In both species, however, variation in size occurs. They are of a pale pinkish colour, when seen in the mass by reflected light. Figs. 1 and 2, Plate V, show in dorsal and lateral views an actively swimming larva thirty-one hours old. Twenty-four hours later (Plate V, Figs. 3 and 4) the hood-fold is becoming prominent, the dorsal gap in the prototroch has formed and four provisional bristles are present in each bundle. The larva is still very granular, but the pigment is already grouping itself into chromatophores which are just like those of *S. alveolata*. The fully developed trochophore stage is represented in ventral view in Fig. 5, Plate V. It cannot be distinguished from that of the preceding species and it develops its bristles and eye-spots in just the same way. Fig. 6, Plate V, shows an early metatrochophore three weeks old. If it be compared with the corresponding stage of *S. alveolata* (Plate I, Fig. 9), a slight difference will be noticed in the form of the trunk and especially in the way in which the telotrochal swelling is marked off from the rest of the body. This difference appears, on the whole, to be constant, but considerable variation exists and it is of no practical service in separating the larvæ of a mixed culture. It is, moreover, difficult to observe in active larvæ and it disappears when the larvæ are fixed. It might be thought that the bristles would show some distinction, but none has been detected. Figs. 7 and 8, Plate V, show in lateral and ventral views a larva two months old. This stage is usually reached much earlier, but in both species the time taken by different individuals of the same culture under apparently identical conditions (i.e. in the same bowl or plunger jar) varies very greatly without any visible effect on the structure. In the lateral view the grasping cilia are represented as holding some of the bristles. The tentacles are just budding out a little posterior to the end of the anterior row of prototrochal cilia.

The larva shown in Fig. 1, Plate VI, was from the same culture and plunger jar as the one just described, but it was only one day older. It was a particularly fine large specimen. At this stage it is approaching the end of its pelagic existence, and the primary chætæ of the crown are already well developed among the bases of the provisional bristles. These chætæ differ markedly from those of *S. alveolata*, and once they have appeared larvæ of the two species are separated with ease. The paleæ (Plate IX, Fig. 1) which correspond to the broad flattened forms of *S. alveolata* are here longer and narrower and are strongly toothed along the margins. They are not flattened, but are rounded into a trough-like shape. The drawing is from a rather flattened specimen. In addition to ten or eleven of these in each bundle two pointed bristles (Plate IX,

Figs. 6 and 7) are also present. The parathoracic parapodia have four bristles, two prominent (Plate IX, Fig. 8) and two inconspicuous (Plate IX, Fig. 9) in each dorsal bundle, while each of the third pair have also a long barbed bristle, of similar function to that of the other species. On these segments the ventral bundles, consisting of two fine bristles each, have appeared. The abdominal parapodia consist of the dorsal uncinigerous lobes only. Each of the first pair of lobes has about eight uncini (Plate IX, Fig. 10), the second pair about four, and the third pair about three, the actual numbers varying as in *S. alveolata.*

(b) *Metamorphosis and the early bottom stages.*

Development of the larva continues a little further until it is ready to metamorphose at a stage in development closely corresponding to that at which *S. alveolata* metamorphoses. Fig. 1, Plate VII, shows the ventral aspect of a larva in which the hood is just commencing to shrink back. This and all succeeding drawings (except Fig. 2, Plate VII) are from larvæ picked out of the plankton at a late stage and which metamorphosed in finger bowls, but all (except Fig. 2, Plate VI, and Fig. 1, Plate VIII) have afterwards been carefully checked on larvæ reared from the egg. In any case, there is not the least doubt as to the species, the crown paleæ being absolutely distinctive.

Fig. 2, Plate VII, is a dorsal view of the anterior region of a metamorphosing larva reared from the egg and over four months old. The great chæta-sacs are turning forwards. This process has almost been completed in the specimen drawn in Fig. 3 on the same plate. In the latter specimen the telotrochal swelling is flexed ventrally and the anus is on the apex of a slight cone. In some individuals at this stage the caudal appendage may be quite long. The prototroch has gone, but the telotroch remains, although its cilia are disappearing. The worm had a mucus tube which was attached to the bottom of the bowl. This is the most advanced stage to which this species has been reared from the egg. The single specimen reared as far as this was nearly fifteen weeks old.

Later stages have been obtained by rearing larvæ from the plankton. Fig. 2, Plate VI, is a ventral view of the head region of such a stage. The " palps " are only just arising, but as in *S. alveolata* there is considerable variation in the time of appearance. The hood has shrunk to very small proportions and is represented by a darkly pigmented patch anterior to the mouth. Above it is the ciliated anterior conical projection or " snout."

A dorsal view of the most advanced specimen obtained is shown in Fig. 1, Plate VIII. It is especially interesting in that the primary crown paleæ have been replaced by a secondary set. The new paleæ of the outer row have the appearance shown in Fig. 2, Plate IX, and they resemble

somewhat the adult paleæ of the same row. There are six of these paleæ on the left and eight on the right side, but the crown was slightly damaged by clogging masses of diatoms when the specimen was obtained, and some may have fallen out. Inside the outer row other paleæ are present. These are three in number (Plate IX, Figs. 3, 4, and 5) and they are rather like the paleæ of the inner two rows of the adult. Unfortunately, owing to the way in which the crown was damaged, their actual positions in the crown are uncertain. A curved bristle is present in the inner side of each peduncle, as in *S. alveolata*. The parathoracic parapodia contain about five bristles in each dorsal bundle. The first pair of abdominal uncinigerous processes have about twenty uncini each, the second pair about eleven each, and the third pair five or six each. The number of chætæ in the ventral bundles of all segments is doubtful, but there are most probably two or three bristles in each ventral bundle of the parathoracic segments and one bristle in each ventral abdominal bundle. A pair of small swellings (only one is visible in the drawing), just anterior to the shrinking telotrochal swelling, may possibly be the developing fourth pair of uncinigerous processes, but if so, they are in a rather different position from the similar swellings in *S. alveolata*. A nototroch is present close to the posterior border of each segment, and a short one exists between the two pairs of eye-spots. As in the allied species, after metamorphosis, the anterior pair of these are closer together and situated more ventrally than the posterior pair.

Two young worms were obtained in which each peduncle of the crown carried one or two paleæ of the secondary type (Plate IX, Fig. 2). These were situated at the dorsal end of the curved outer row, the remainder of the paleæ in the row all being of the primary type (Plate IX, Fig. 1). We may perhaps conclude from this that the primary paleæ fall out and are replaced in regular sequence starting from the dorsal end of the curved row.

The building operations of this species have not been observed.

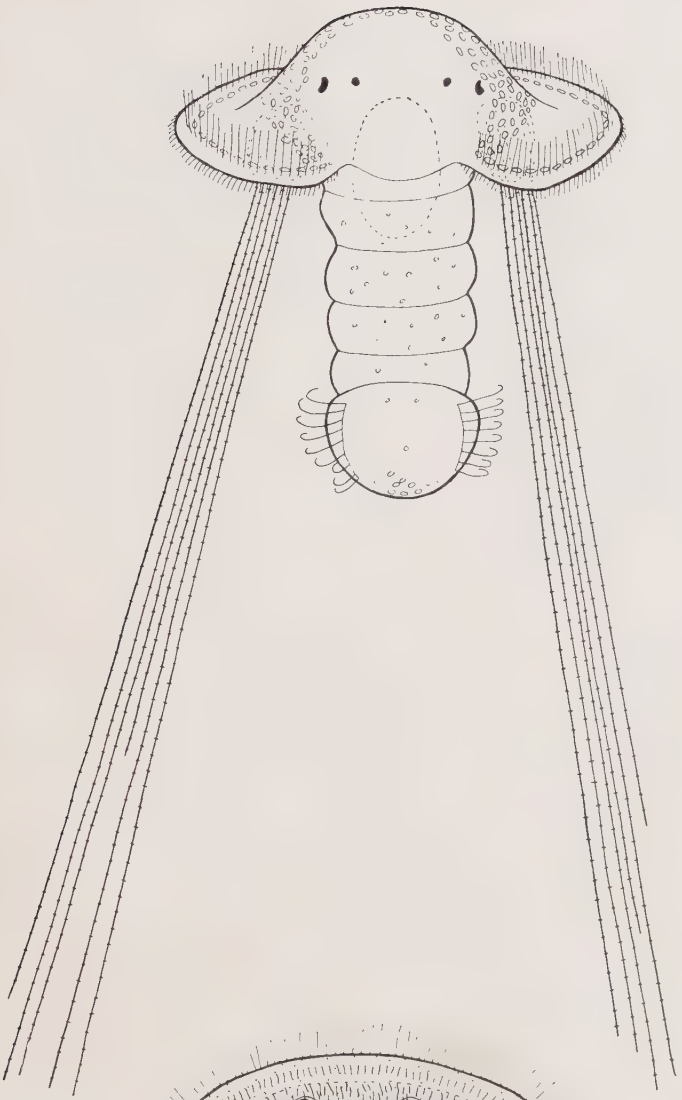
5. THE LARVA OF *PALLASIA MURATA* ALLEN.

Besides the two species of Sabellaria, the larvæ of which have just been described, one other Sabellarian has been recorded for the British Isles. This is the rare *Pallasia murata*, which has been described by Allen (**1**) as occurring in the neighbourhood of Plymouth, and of which only a very few specimens have been obtained, although the empty tubes are moderately common. Very little is known concerning the larval stages, but Caullery describes and figures (**3**, p. 172, and Fig. 3) a larva which he found in the plankton at Wimereux and which almost certainly belongs to this genus and most probably to the species also. It was in an advanced stage

of development with primary crown chætæ at the base of the dorsal part of each bundle of provisional bristles. One of these chætæ was a strong hook resembling closely the hook present on the dorsal surface of each peduncle of the adult Pallasia. Close by each chæta-sac were about ten tentacular cirri, probably the papillæ which form a row along the external margin of each adult peduncle, and corresponding to similar papillæ in Sabellaria, in which only two are found by each chæta-sac in the later pelagic and early bottom stages. Four parathoracic segments were present, a feature in which Pallasia differs markedly from Sabellaria, where there are only three. The larva had also nine pairs of uncinigerous processes instead of only three as in Sabellaria larvæ. The anal cone, corresponding to the telotrochal swelling in Sabellaria, is of special interest in that, posterior to the telotroch, it presented fine transverse constrictions which may represent segments that will form the caudal appendage. There can be little doubt, after a consideration of these points, that this larva was indeed the larva of Pallasia, as Caullery demonstrated. It may be that his earlier larvæ also belong to the same genus, but this is at present impossible to decide. The pigment on the back, which in the Sabellaria larvæ described in this paper was very dark brown, or black in general appearance, is referred to by Caullery as "violacé" in both his early larvæ and in his Pallasia larva. This may or may not prove to be a distinction between the two genera.

Towards the end of February, 1927, at the very beginning of the present observations, and while engaged in picking out from the plankton Sabellaria larvæ which were at that time thought to be some form of Spionid, a single larva of the same type, but of a strikingly different general appearance, was obtained. Rough sketches of the dorsal aspect and of the mouth region in ventral view of this larva were made at the time and are reproduced in Text-Figs. 4 and 5. The larva was not observed in any great detail in case prolonged confinement in a cavity-slip should kill it, for it was hoped to rear it to a stage at which the genus, at least, could be determined. Unfortunately these hopes were not realised, and the larva subsequently died without further development. Since then the searching of many plankton catches has failed to yield another specimen. These rough sketches, however, have now a special interest, for it is very probable that this is the larva of *Pallasia murata* Allen. That assumption is based on the fact that *P. murata* is the only species of Sabellarian besides *S. alveolata* and *S. spinulosa* which has been recorded from anywhere reasonably close to the British Isles, and it is known to occur on grounds close to where this particular and distinctly Sabellarian larva was caught.

The larva was much bigger than the corresponding stage of Sabellaria, and the provisional bristles were longer and straighter. The hood and



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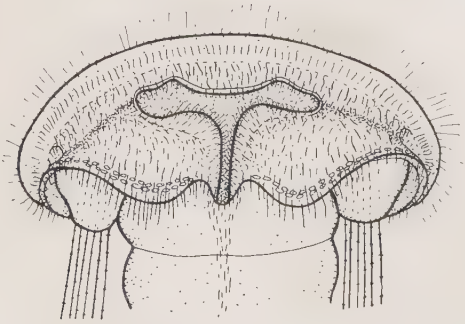

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TEXT-FIGS. 4 and 5.—Dorsal view, and ventral view of mouth region, of a Sabellarian larva which is probably the larva of *Pallasia murata* Allen. Sketch from life × 156. Actual length (excluding bristles) approx. 410μ.

lip-folds were more highly developed than they are in Sabellaria, but in their essential structure they were the same. Chromatophores of a beautiful pale green colour were scattered over certain regions of the hood and arranged in a row just anterior to the prototroch. Two pairs of eye-spots were present. The ciliation appears to have been the same as in Sabellaria. The manner in which the telotroch is drawn is interesting; the cilia shown are obviously grasping-cilia. No driving cilia are represented although it is highly probable that some were present. This drawing was made before the grasping-cilia in Sabellaria had been observed and at the time their function was certainly unsuspected.

In two points this larva can be compared with Caullery's latest stage. Thus the extra development of the hood-fold is indicated in his drawings (**3**, Fig. 3). Secondly, Caullery writes of the chromatophores as being yellow in colour, but the colour may change with age, as it does to some extent in Sabellaria, where the chromatophores gradually become darker brown when viewed as a whole.

6. KEY TO THE BRITISH SABELLARIAN LARVÆ.

It is now possible to construct a tentative key which will enable plankton workers to distinguish the later pelagic stages of the three British species of Sabellarians.

1. Provisional bristles less than 400μ long. Hood-fold fairly prominent. Chromatophores brown or yellow in general appearance.....2
   Provisional bristles approx. 760μ long. Hood-fold very prominent. Chromatophores a beautiful pale green colour or possibly yellow in the later stages.....3
2. Primary crown chætæ, which appear among the bases of the provisional bristles during the later stages, very broad and flat, very slightly toothed (Plate IX, Fig. 12).....*S. alveolata*
   Primary crown chætæ long, slightly trough-shaped, of moderate width and very strongly toothed along both edges (Plate IX, Fig. 1) *S. spinulosa.*
3. In addition, during later stages, a strong hook by the base of each bundle of provisional bristles; four parathoracic segments and more than three pairs of uncinigerous lobes.....*Pallasia murata.*

It is at present impossible to separate the early stages of the two species of Sabellaria.

7. PREVIOUS RECORDS OF SABELLARIAN LARVÆ.

De Quatrefages appears to have been the first to record the eggs and larvæ of Sabellaria. In 1847 he published a short paper (**17**) dealing mainly with fertilisation and the fertilisation membrane, followed in the next year by a longer paper (**18**) discussing those subjects in great detail, and containing also an account and figures of the segmentation and the early larvæ of a species of Sabellaria. He figures the prototroch as a wide band of cilia, which was entirely lost in his latest stage with four bristles on each side. At this stage his larvæ died. In 1850 he published another paper (**19**), describing various experiments on the artificial fertilisation of Sabellarian ova. No further work on this subject was published until 1881 when Horst (**12**) described his researches on the early development of *S. alveolata*. A short extract (**13**) of this paper was brought out about the same time. A plate of figures accompanied the longer paper, most of them concerned with the segmentation stages, in which Horst disagrees with the account given by de Quatrefages. A figure of the trochophore is also given on this plate with the chromatophores shown in colour. The colouring is quite good. He has, however, failed to distinguish the hood-fold from the lip-fold; they are shown as if they were fused into one. The strong forward arching of the prototroch over the mouth does not exist in a free-swimming larva, but might be caused by pressure beneath a cover-glass. In 1885 von Drasche (**5**) described the segmentation and early stages of *S. spinulosa*. His figure of the trochophore is also coloured, but, while he illustrates the greenish yellow ground colour of the chromatophores quite faithfully, in only two of them does he show the brown specks. A single eye-spot is shown, but is placed on the right side instead of on the left. During the present research this single eye-spot which appears first has never been seen on the right side, but always on the left. Several prototrochal rows of cilia are drawn with the cilia in the posterior rows about as long as in the anterior row. He does not seem to have realised the presence of the hood-fold, and the lip-folds are drawn to appear as though they pass below instead of above the provisional bristles. It is also interesting to note that he states that the fertilisation membrane ("Eimembran") is lost and does not form the cuticle of the larva. Nothing further was known until 1914, when Ziegler published another account (**21**) of the segmentation and early larvæ of *S. spinulosa*. He gives figures of the trochophore stage with six bristles in each bundle, in which he indicates the hood-fold. In the same year Caullery published his valuable paper (**3**), pointing out the chief characters of Sabellarian, as distinct from Spionid larvæ. This paper has already been frequently referred to. Since that time no further work on Sabellarian larvæ has been published, except that McIntosh

has given some outline figures (**15**, Plate XCIV) of larvæ which probably belong to this group. Unfortunately there appears to have been some confusion in the numbering of this plate. Figs. 8 and 9 are probably Sabellarian larvæ; the former is stated to be a Spionid larva, while Fig. 9 is not referred to. Figs. 10 and 11 are stated to be probably Sabellarian larvæ; the former is certainly not, but the latter may be. There is no Fig. 11*a*. Some of this numbering was corrected in a later volume (**16**, p. 5).

In addition to the foregoing publications where Sabellarian larvæ are referred to as such there exist a number of papers containing figures of larvæ which almost certainly belong to the Sabellariidæ, although they are usually described as some form of Spionid. Busch, as early as 1851, figures these larvæ (**2**, Taf. VII, Figs. 5–8), which he obtained off Heligoland, the Orkneys, Cadiz, Malaga, and Trieste, but he does not name them. Fewkes (**7**) gives three figures (Plate II, Figs. 1–3), and describes them under the name of Spio sp. without giving any reasons for attributing them to that genus. He obtained his larvæ at Newport, U.S.A. Häcker also described and figured (**11**, p. 16, Taf. II, Figs. 14 and 15) similar larvæ from the west coast of Africa, and likewise called them Spio. Caullery has already suggested that the larvæ of these three authors were really Sabellarians. Both Fewkes and Häcker refer to a paper by Leuckart and Pagenstecher (**14**) who give figures of different stages of a larva which, without bringing forward any real evidence, they had referred to Spio in the following words: "Es handelt sich hier ohne Zweifel um eine *Spio*, deren Charaktere sich jedoch nicht so weit ausbildeten, dass sie eine Artunterscheidung mit Bestimmtheit gestattet hätten." They believed the species might be *Spio crenaticornis* on account of the similarity of the tentacle wrinkles of that species and those of their latest larva, and also because *S. crenaticornis* was common in Heligoland where their larvæ were obtained. Their figures (Taf. XXIII, except Fig. 1), however, show the Sabellarian characters; even a few primary crown paleæ are indicated among the provisional bristles of their oldest stage. In the latter, it is true that five pairs of parathoracic parapodial bristle bundles are shown and no abdominal uncinigerous lobes, but the other characters, including the general shape, are so certainly Sabellarian that this can be regarded as an error of observation. Thus the responsibility of being the first to attribute Sabellaria larvæ caught in the tow-net to the genus Spio appears to rest with these joint authors and their identification was later accepted by both Fewkes and Häcker.

Claparède's early Leucodora (Polydora) larvæ (**4**, Taf. VII, Figs. 4–5) were also very probably trochophores of Sabellaria, at a stage when they had got nine or ten bristles in each bundle and before the trunk region

had begun to be definitely segmented. As was pointed out in a previous paper (Wilson, **20**) Gravely (**9**, p. 46), accepting these figures and also Fig. 6 on the same plate as the larvæ of Polydora, described as metatrochophores of that genus some larvæ which he had found on several occasions in the July plankton at Port Erin. His description of these metatrochophores (which were only examined in the fixed contracted condition), so far as it goes, corresponds very well, except for one point, with Sabellaria larvæ, and not at all to Claparède's Fig. 6, Taf. VII, as Gravely himself seems to have realised. The point in which the description does not correspond is in the length of the provisional bristles, which are stated to be 850μ long, which would make them longer than the bristles of Pallasia. These bristles are described as ringed, but it is not stated that the rings (collars) were toothed. In another paper Gravely repeats Claparède's figure (**10**, Text-Fig. 3a), and uses it in a discussion on the probable mode of development of the vestibule in Polydora. If, as is highly probable, this larva is really Sabellaria, then the notch shown in the prototrochal rim in the neighbourhood of the mouth would indicate the lip-folds. The ciliated œsophagus is represented as running in an anterior direction just as it does in Sabellaria larvæ. In any case this larva and Gravely's metatrochophores are certainly not Polydora. The same remark applies to the metatrochophore figured by Flattely (**8**, Fig. 1) who, following Gravely's description, called it Polydora. The figure shows the Sabellarian characters.

8. NOTE ON THE CAUDAL APPENDAGE OF SABELLARIA.

Comparatively little appears to be known of the internal structure of the caudal appendage. This smooth achætous posterior region is usually stated to be "unsegmented." Externally at all events that does, indeed, appear to be the case, but sections reveal the presence of a number of transverse septa, fifty or sixty in number, in the adult *S. alveolata*. The gut is fused to the dorsal and lateral body-walls of the appendage, but on the ventral side the two are separated by a space. The septa cross this space at regular intervals. The space is further divided by a median longitudinal mesentery which runs down the whole length of the appendage. These septa, the well-developed blood vessels associated with them, and the caudal appendage generally, were observed by the late Mr. Arnold T. Watson, whose original notes of an extensive series of observations, spread over many years, on the anatomy of the British species of this genus, I have been privileged to consult through the kindness of Mrs. Watson and Professor Fauvel. If these septa delimit true segments, and there appears to be no reason to suppose that they do not, then the caudal appendage is really a segmented

structure composed of fifty or sixty segments. In development it arises from the posterior part of what has been termed the telotrochal swelling. It appears that it is from the region immediately anterior to this swelling that new chætigerous segments are produced, and that the greater part of the swelling shrinks away when the pelagic life is over. The telotrochal swelling, as a whole, cannot therefore be properly termed a pygidium, and it is for this reason that the former term has been used here.

Sections have been cut of the caudal appendage at the stage when it was growing out during metamorphosis, but the scarcity of material has rendered it impossible to give an account of the development of the internal structures.

9. SUMMARY.

1. *Sabellaria alveolata* Linnæus has been reared for the first time from the egg through the pelagic stages and metamorphosis to early bottom stages. The chief features in the development of the external characters are described and special attention is drawn to the existence of peculiar grasping-cilia on the telotroch. The manner in which the young worm builds its first tube of sand grains is also described.

2. *Sabellaria spinulosa* Leuckart has similarly been reared for the first time from the egg to early bottom stages. Its development is very similar to that of the preceding species, but during the later pelagic life the two can easily be separated, as the primary paleæ of the crown, which appear among the long provisional bristles of the first pair of parapodia, show a marked specific difference. The early stages cannot be distinguished.

3. A larva which is probably that of the rare *Pallasia murata* Allen is described.

4. A tentative key to the British Sabellarian Larvæ is drawn up.

5. The observations of previous workers are discussed. It is shown that Sabellarian larvæ have frequently been described as the larvæ of Spio or of Polydora, in spite of the fact that the early stages of Sabellaria had been obtained more than once from artificial fertilisations. Caullery was the first to point out the error, and he is fully confirmed in this paper.

6. It is shown that the caudal appendage of a full-grown *Sabellaria alveolata* possesses internally a series of fifty or sixty transverse septa.

10. APPENDIX.

The following is an original note, by the late Mr. Arnold T. Watson, which is of special interest in that it describes early bottom stages of *Sabellaria alveolata* only a little more advanced than the latest stage to which I have been able to rear my worms. The note is dated October 16th, 1915, and apparently refers to a mass of tubes and living worms of this species which were received at Sheffield from Seascale on October 7th.

" The mass received is in a very healthy condition and in parts was encrusted with numerous very young specimens—some slightly older than others. In all young specimens a median ciliated process arises between the two opercular lobes. In the youngest it was clearly seen arising separately a short distance behind the upper lip, and the membrane joining the lobes was further still from the back of the upper lip. In older ones the ciliated process seems adhering to the membrane. There is at this stage (when the worm would be about 1·1 mm. long and have three tentacles at each side in addition to the two central tentacles) an " eye-spot " at each side of the central ciliated process and through the dorsal face two other larger eye-spots—situated nearer the mouth—can be clearly seen. When the worm bends its peristomial lobes to form a right-angle with its body both sets of eye-spots can be seen in top view forming a square. The papillæ external to the paleæ (about three or four on each side) are much longer in proportion than in the adults, and some of them (possibly all) are tipped with " tactile (?) hairs." The young Sabellarians in situ are difficult to see ; as in this specimen the lobes look like black specks and correspond closely with adjoining black sand-grains.

" A young specimen about 1·1 mm. long when extended alive has two tentacles on each side of the peristomial lobes (in addition to the two long median tentacles) and three cirri just below the paleæ, viz. : one long one at the dorsal edge and one at the ventral end of the crescent and one intermediate between the two—each with ' tactile hairs.' Two dorsal eye-spots about the level of start of long tentacles. The median ciliated process is very evident but difficult to tell whether it was above or under the membrane."

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PLATE I.

Larvæ of *Sabellaria alveolata* Linnæus. All drawings from life × 156. All measurements exclude apical cilia and bristles.

Fig. 1.—Free-swimming embryo 27 hours after fertilisation. Actual length approx. 95μ (see page 223).

Fig. 2.—Embryo 46 hours after fertilisation. Actual length approx. 95μ (see page 224).

Fig. 3.—Embryo 61 hours after fertilisation. Actual length approx. 100μ (see page 224).

Fig. 4.—View of right side of the same larva as shown in Fig. 3.

Fig. 5.—Larva 91 hours old. View of left side. Actual length approx. 100μ (see page 225).

Fig. 6.—Ventral view of the same larva as shown in Fig. 5.

Fig. 7.—Larva about five and a half days old. View of left side from a slightly ventral position. Actual length approx. 100μ (see page 225).

Fig. 8.—Larva about twenty days old. View of right side. Actual length approx. 165μ (see page 228).

Fig. 9.—Ventral view of the same larva as shown in Fig. 8.

Fig. 10.—Larva about six weeks old. Dorsal view. Actual length approx. 310μ (see page 223).

Fig. 11.—Ventral view of the same larva as shown in Fig. 10.

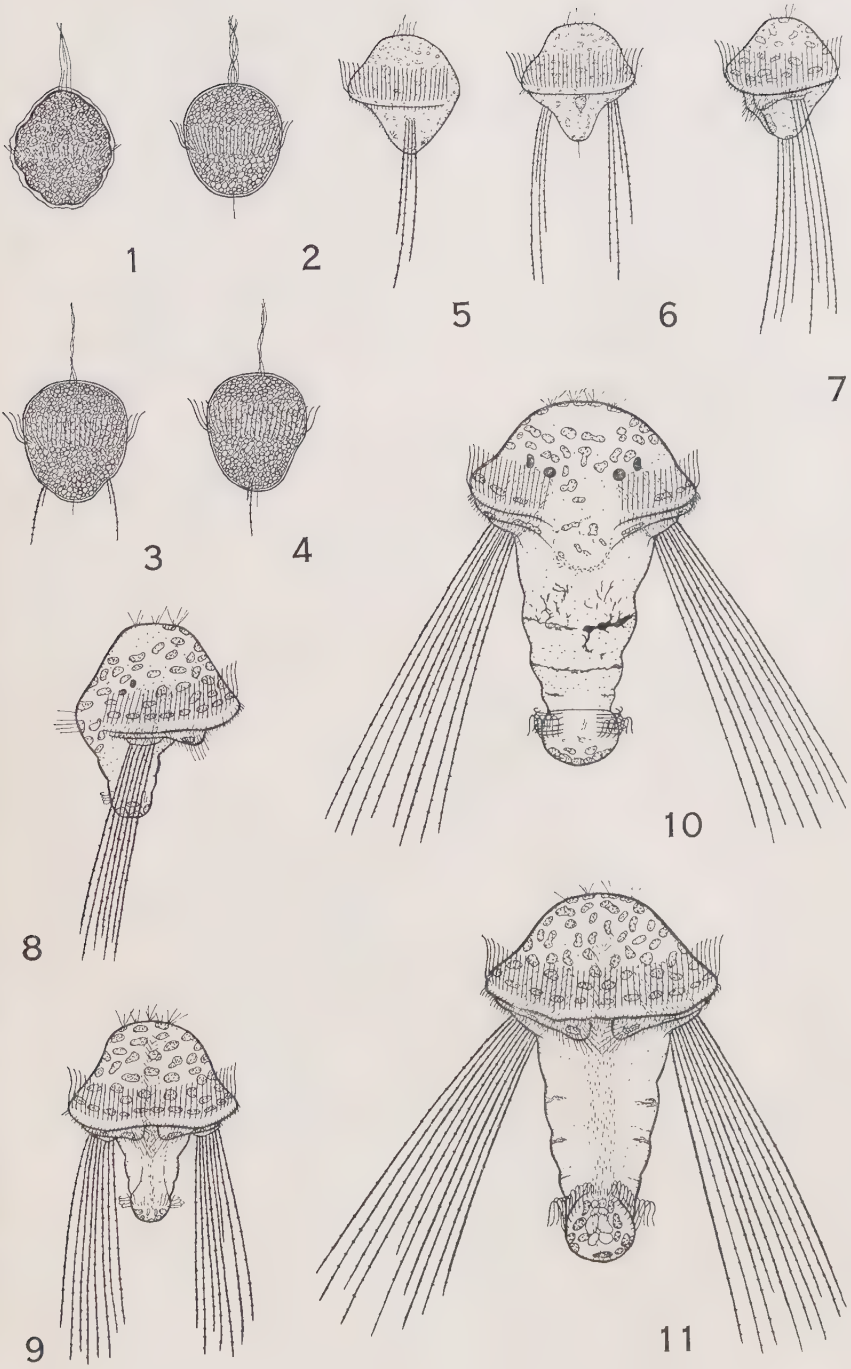
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PLATE II.

Larvæ of *Sabellaria alveolata* Linnæus. All drawings from life × 156. All measurements exclude apical cilia and bristles.

Fig. 1.—Larva just over six weeks old. View of right side. Actual length approx. 435μ (see page 229).

Fig. 2.—Larva just over seven weeks old. View of right side. Actual length approx. 435μ (see page 229).

Fig. 3.—Larva about seven and a half weeks old. Dorsal view. Actual length approx. 500μ (see page 230).

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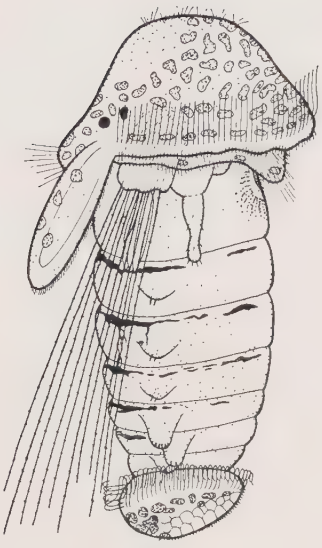

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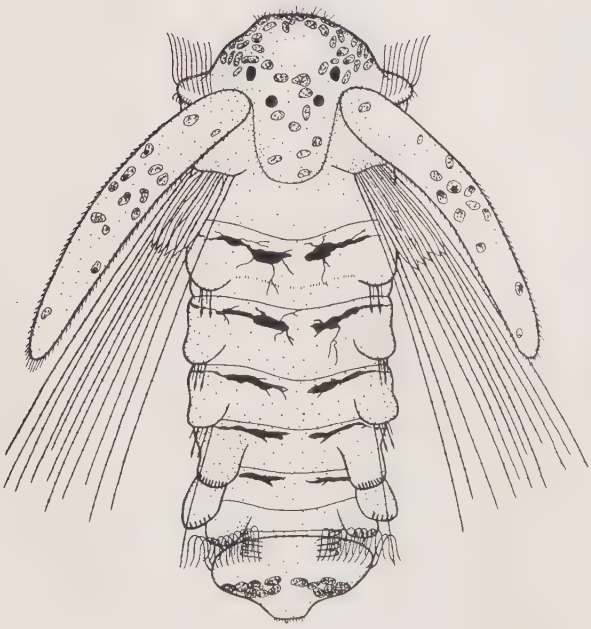

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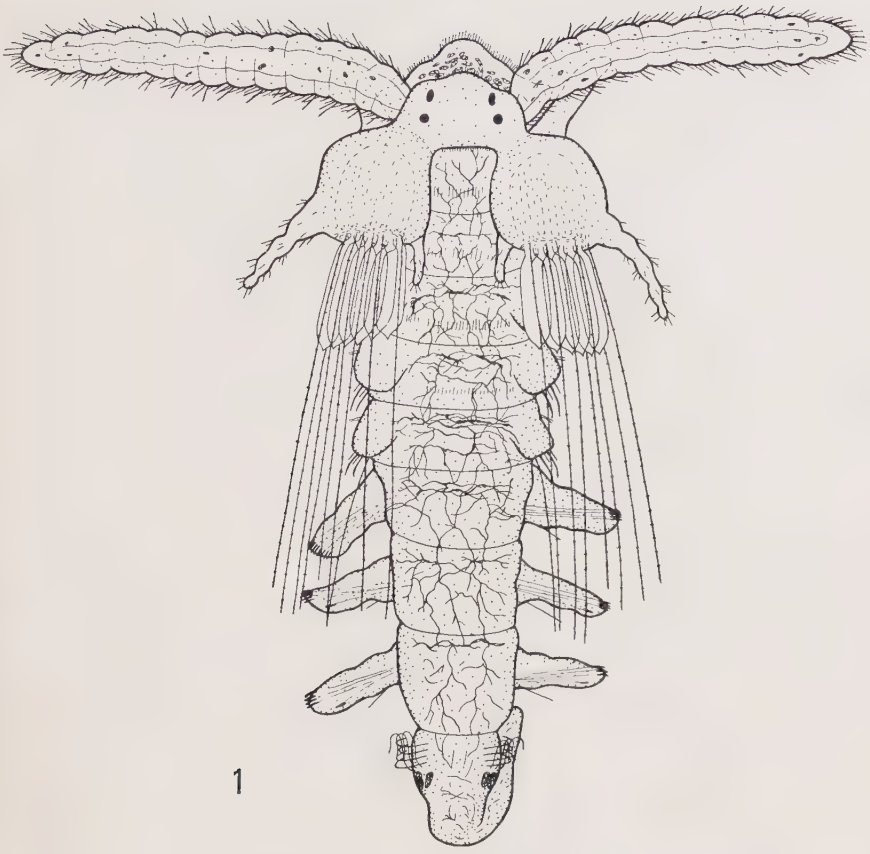
PLATE III.

Larvæ of *Sabellaria alveolata* Linnæus. All drawings from life × 156.

Fig. 1.—Dorsal view of metamorphosing larva about six and a half weeks old. Actual length, from anterior extremity of head to posterior bend, approx. 665μ (see page 234).

Fig. 2.—Ventral view of head region of larva just commencing to metamorphose. Stage earlier than that shown in Fig. 1 (see page 233).



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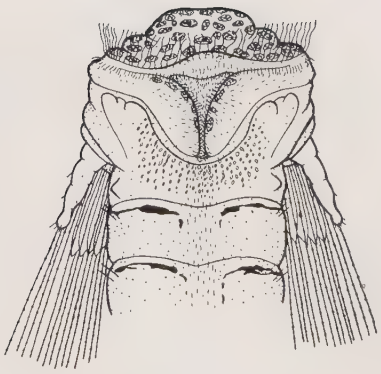

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PLATE IV.

Ventral view of early bottom stage of *Sabellaria alveolata* Linnæus. Drawn from life $\times 156$. Age just over seven weeks after fertilisation. Actual length, from tip of snout (seen between the peduncles) to posterior flexure, approx. 780μ (see page 234).

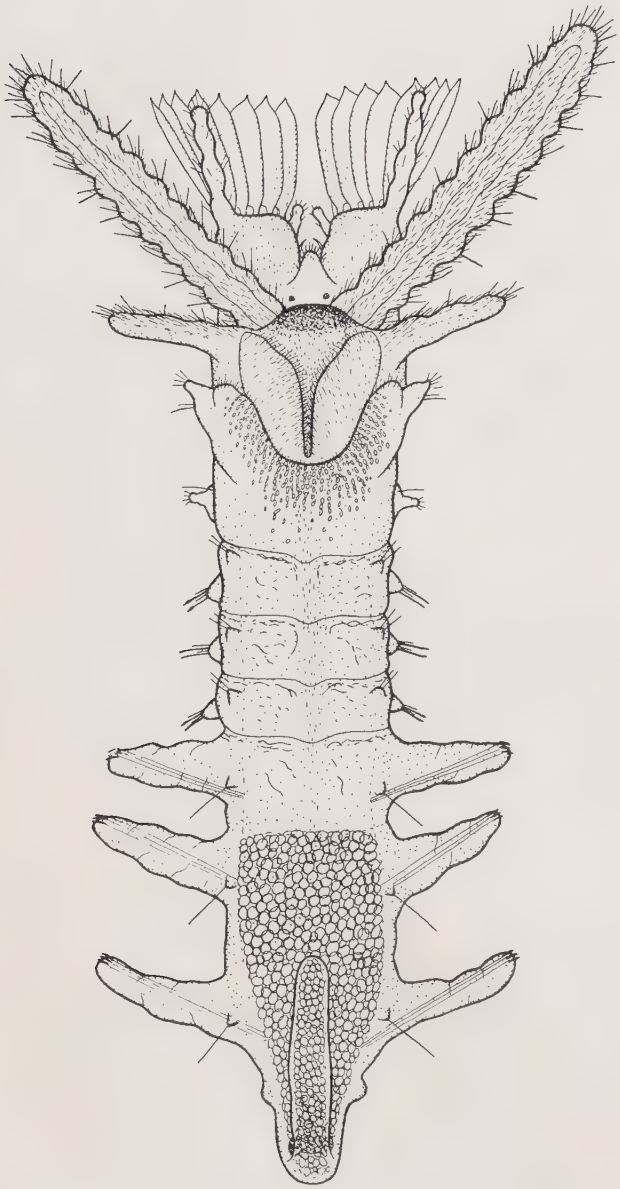

PLATE V.

Larvæ of *Sabellaria spinulosa* Leuckart. All drawings from life × 156. All measurements exclude apical cilia and bristles.

Fig. 1.—Free-swimming embryo 31 hours after fertilisation. Dorsal view. Actual length approx. 90μ (see page 239).

Fig. 2.—View of left side of the same embryo as shown in Fig. 1.

Fig. 3.—Embryo 55 hours after fertilisation. View of right side. Actual length approx. 90μ (see page 239).

Fig. 4.—Ventral view of the same embryo as shown in Fig. 3.

Fig. 5.—Larva just over four days old. Ventral view. Actual length approx. 90μ (see page 239).

Fig. 6.—Larva about three weeks old. Ventral view. Actual length approx. 180μ (see page 239).

Fig. 7.—Larva about two months old. View of right side. Actual length approx. 370μ (see page 239).

Fig. 8.—Ventral view of the same larva as shown in Fig. 7.

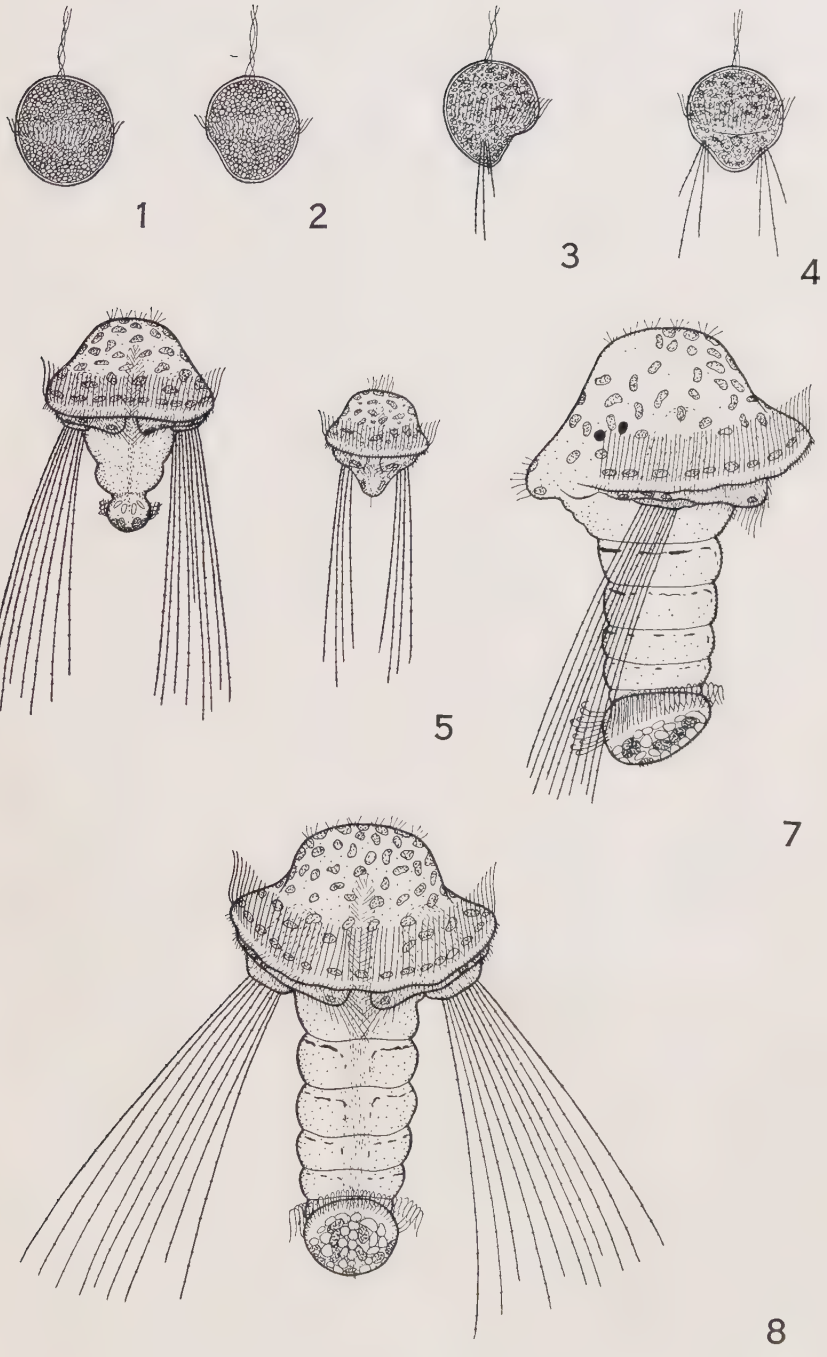
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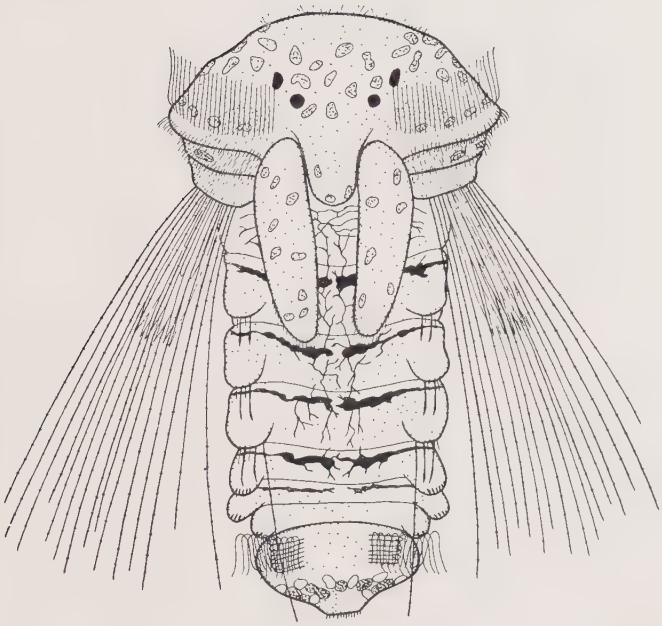
PLATE VI.

Larvæ of *Sabellaria spinulosa* Leuckart. Drawings from life × 156.

FIG. 1.—Larva about two months old. Dorsal view. Actual length approx. 500μ (see page 239).

FIG. 2.—Ventral view of head region of a metamorphosed early bottom stage (see page 240).



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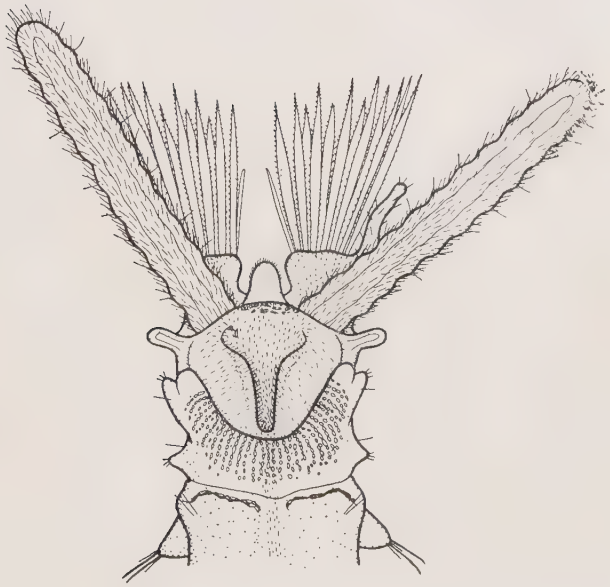

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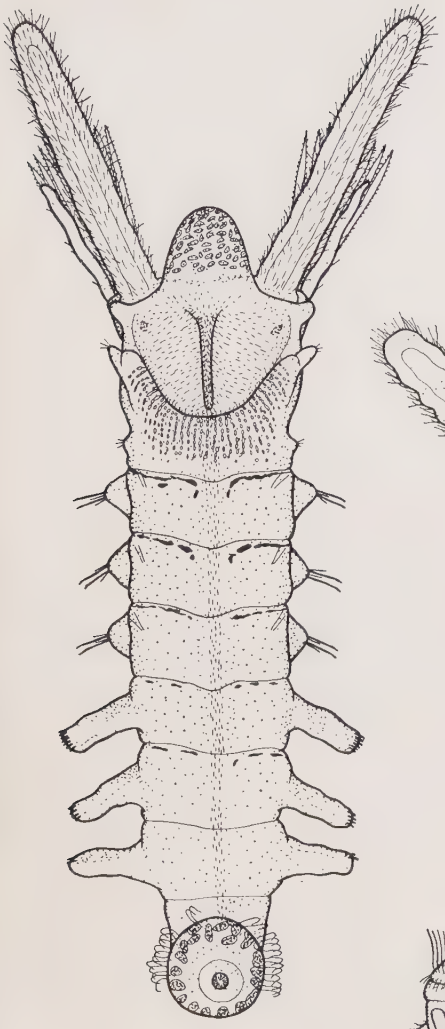
PLATE VII.

Larvæ of *Sabellaria spinulosa* Leuckart. Drawings from life $\times 156$.

Fig. 1.—Ventral view of anterior end of a larva just commencing to metamorphose (see page 240).

Fig. 2.—Dorsal view of anterior end of metamorphosing larva about four months old (see page 240).

Fig. 3.—Ventral view of metamorphosing early bottom stage. The drawing is from a specimen picked out from the plankton before it was ready to metamorphose. A single specimen has been reared from the artificially fertilised egg as far as this stage with which it corresponded in every important particular. It was then nearly three and a half months old. Actual length (excluding tentacles) approx. 670μ (see page 240).



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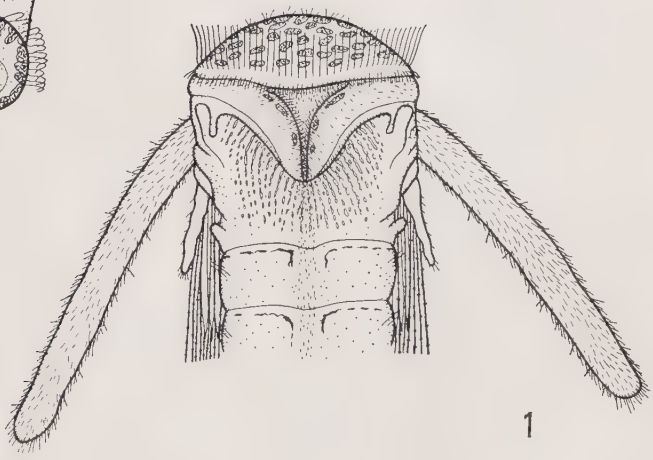

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PLATE VIII.

FIG. 1.—Early bottom stage of *Sabellaria spinulosa* Leuckart. Dorsal view from life ×156. Actual length, from tip of snout (seen between the peduncles) to posterior flexure, approx. 665μ (see page 240).

FIG. 2.—Mucus and first sandy tube of early bottom stage of *Sabellaria alveolata* Linnæus ×39. Actual length of sandy portion about 1·9 mm. (see page 238).

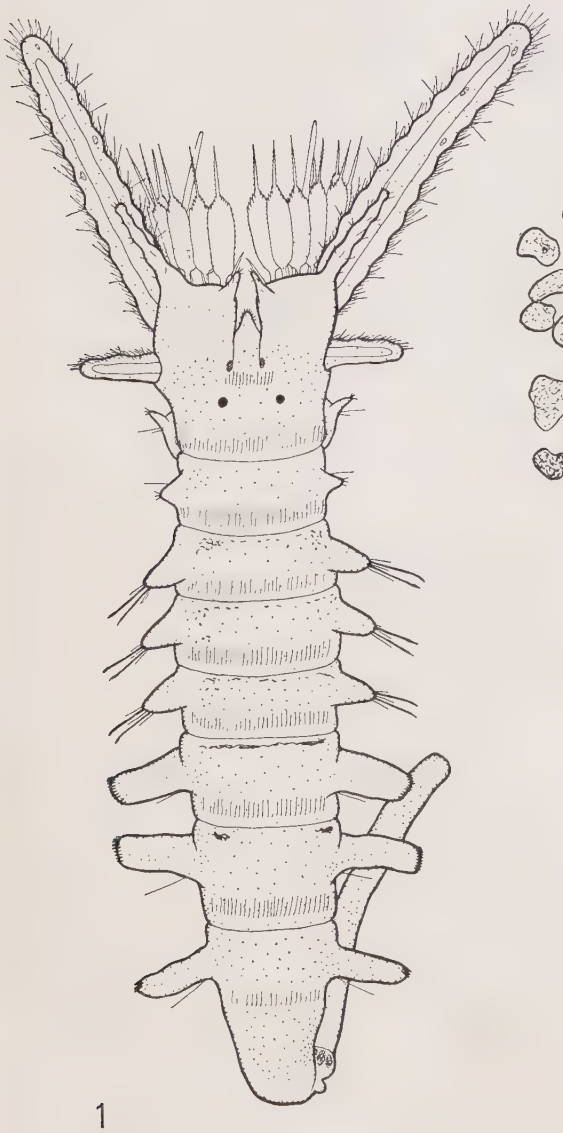

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PLATE IX.

All drawings, except Fig. 19, $\times 620$.

A. Chætæ from larvæ and early bottom stages of *Sabellaria spinulosa* Leuckart.

Fig. 1.—One of the primary crown paleæ.

Fig. 2.—One of the secondary crown paleæ.

Figs. 3, 4 and 5.—Paleæ from one crown of the individual drawn in Fig. 1, Plate VIII.

Fig. 6.—Bristle from crown.

Fig. 7.—Bristle from crown.

Fig. 8.—Spear-shaped bristle from a parathoracic segment.

Fig. 9.—Slender bristle from a parathoracic segment.

Fig. 10.—Uncinus.

B. Chætæ from larvæ and early bottom stages of *Sabellaria alveolata* Linnæus.

Fig. 11.—Portion of ringed provisional bristle.

Fig. 12.—One of the primary crown paleæ.

Fig. 13.—Bristle from crown.

Fig. 14.—Bristle from crown.

Fig. 15.—Bristle from inner side of peduncle.

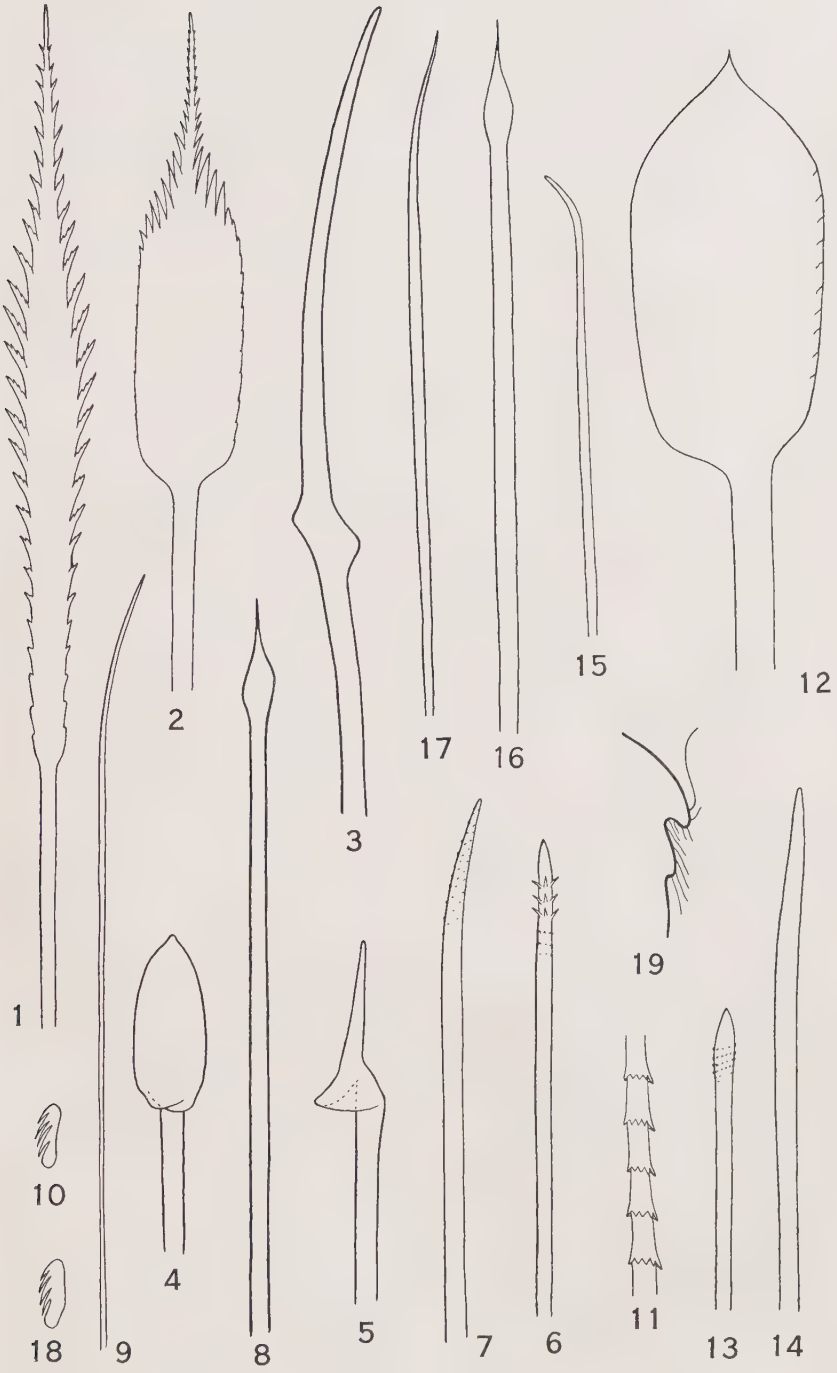
Fig. 16.—Spear-shaped bristle from a parathoracic segment.

Fig. 17.—Slender bristle from a parathoracic segment.

Fig. 18.—Uncinus.

C. Hood and lip-fold of *Sabellaria alveolata* Linnæus.

Fig. 19.—Diagrammatic section through prototroch of an early larva to show roughly the extent of folding at the sides of the body.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On the Cœlomic Cilia and Circulation of the Body-Fluid in *Tomopteris helgolandica.*

By

Dr. Anton Meyer.

With 1 Figure in the Text.

A. INTRODUCTION.

The œcological significance of cilia and ciliary currents has been studied hitherto mainly so far as they are connected either with the epidermis or with the intestine. Epidermal cilia produce currents by which either the animal itself is moved or the surrounding medium is carried over the surface of the unmoved animal. In the latter case the ciliary currents serve for collecting substances, ordinary food and oxygen. It may be said, that the degree of specialisation of epidermal cilia generally indicates the degree of intimate dependence of the animal on its outside conditions (natural surroundings). (The cases where epidermal cilia are connected with sense organs are comparatively few.)

Intestinal cilia have a more limited significance : they never serve for movement of the animal nor for sensory functions, but are probably restricted to aiding the absorption of chymus and of oxygen by moving the content of the intestine. Since the ciliated intestinal surfaces are neither fully exposed to the outside conditions nor completely closed from the latter, we may express their position as semi-inside or internal.

Besides the epidermal and entodermal layers there is a third layer which builds up the architecture of many classes of animals and which resembles the first two layers in its epithelial character and in the possession of an extensive free surface ; it is the cœlomic epithelium which surrounds the body cavity and is well developed in the Echinoderms, Chætognatha, Brachiopoda, Phoronidea, Bryozoa ectoprocta, Sipunculoidea, and Annelids. The cœlomic cavity indeed is thus the innermost part of these animals ; it is the place of sexual reproduction, and holding an intermediate position between the nutritive organs on the one side and the muscular body wall which produces waste products, it becomes connected with both nutrition and excretion. The sexual products and excretory matters are carried out through the segmental organs ; they represent a cœlomic derivative, the covering with cilia

of which is well known. The remaining parts of the cœlomic epithelium, however, show, in many cases, also a covering with cilia, which may be called cœlomic cilia in the strict sense.

The cœlomic cilia have escaped observation for a long time, and with exception of the Brachiopoda (Morse, 1901*) they have in no case been made the subject of closer examination. As will be seen from the following, the cœlomic cilia may attain a high level of physiological differentiation which is expressed in the regular arrangement and distribution, in the constancy of the direction of the effective stroke of all cilia in a given area, and in the co-ordination of the directions in neighbouring areas. The result of these is a circulation of the cœlomic body fluid which includes more or less the complete body cavity.

Before describing the cœlomic cilia and circulatory currents in a special case, it may be well to establish the positions of cœlomic cilia in relation to the epidermal and intestinal cilia and their œcological significance in the following scheme :—

CILIATED EPITHELIA.

Position in the general architecture of lower animals.	Œcological significance.
I. Outside (external)	Moving the animal (locomotion). Moving the surrounding medium and collecting :— 1. Food (nutrition). 2. Oxygen (respiration).
II. Semi-inside (internal)	Moving the content of the intestine (nutrition, respiration).
III. Fully-inside (inside)	Moving and circulating the cœlomic body fluid (circulation, etc.).

Cœlomic cilia in the Annelids were first specially examined by myself in *Tomopteris helgolandica* (*catharina*) in 1926 and later in full detail in another species from the Mediterranean (*T. elegans*), and also in various other classes (Bryozoa ectoprocta, Chætognatha, Polynoids) 1927.† The species common in the North Sea and the Channel, *T. helgolandica*, is somewhat different from the Mediterranean species ; therefore a special examination of *T. helgolandica* seemed necessary.

A few words on the general structure may be in place.

* Morse, E. S., 1901 : "Observations on Living Brachiopoda." Memoirs Boston Soc. of Nat. Hist., Vol. V.

† Die Segmentalorgane von *Tomopteris catharina* . . . ein Beitrag zur Theorie d. Segmentalorgane, Zeitschr. f. wiss. Zool., 1926.

Über Cölombewimperung u. cölomatische Kreislaufsysteme bei Wirbellosen, *ibid.*, 1927.

B. GENERAL REMARKS ON THE STRUCTURE OF TOMOPTERIS.

The Tomopterids are a family which is entirely restricted to pure planktonic life. Among the Annelid families they are a somewhat outstanding type; in external appearance they are noteworthy for the elongated shape of the parapodia, the fin-shape and purely glandular character of the cirri, the absence of bristles in the segments behind the mouth, also for the great length of a pair of tentacular cirri, for their transparency, and in some cases for the presence of a caudal region (Fig. 1, A). The transparency is due to the entire absence of pigment cells and to the thinness of the muscular layer and absence of connective tissues. The caudal region is a body region which does not reach full development; undoubtedly it is becoming vestigial and is in some species, e.g. *T. elegans*, fully suppressed and has phylogenetically disappeared.

The internal structure is noteworthy owing to the complete absence of transverse dissepiments. Another peculiarity is the absence of blood-vessels, which is connected with the reduced condition of retroperitoneal connective tissue and the conditions of planktonic life.

C. THE CŒLOMIC SYSTEM.

The cœlomic system includes the properties of the cœlom and the segmental organs.

The *cœlomic cavity* forms a continuous space on each side, both sides being separated by the dorsal and ventral mesentery of the gut; the cavity of the trunk region communicates widely with the cavities of the parapodia and so it shows parapodial and interparapodial sections. The mesenteries are wanting in the pharyngeal region, and the cœlomic cavity extends here forwards into the basal region of the head tentacles.

The content of the cœlomic cavity consists mainly of the sexual products, which are easily seen floating after separation from the gonads; the latter are situated in the cavities of the ventral and dorsal cirri of all segments behind the mouth. In the females a great number of oocytes become abortive and finally changed into numerous small plasmatic corpuscles. Those oocytes which develop into eggs are noteworthy through their considerable increase in size. True cœlomic corpuscles I have been unable to observe in *T. helgolandica* (but they are present in *T. planktonis* and *T. elegans*, although very rare). Statements of other authors, that there were a great number of true cœlomic corpuscles are wrong and are due to confusion with abortive oocytes or with spermatocytes.

It is also noteworthy that the secretion of the rosette-like organs (of both

categories) is discharged into the cœlomic cavity and is phosphorescent there. The rosette-like organs (rosettes and hyaline glands) are of mesodermal origin. Those of the second category (=rosettes) are, in young stages, situated in the basal region of the first and second parapodium (only) and are metamorphosed cœlomostomes, still showing in one species, *T. mariana*, their connection with solenocytes and retaining their original position in the basal region, where in the posterior segments (from the 6th onwards) the typical cœlomostomes and solenocytes are situated.

The connection of the cœlomic cavity with the exterior is established through the segmental organs, consisting of a spherical group of solenocytes, a small cœlomostome and a "nephridial" canal; the lumen of the latter can be expanded and contracted. In the females two pairs of large cœlomostomes are developed in the 4th and 5th segments; they are situated in a position which is not homologous with that of the ordinary cœlomostomes and represent a second set of cœlomostomes which is developed *later* in ontogeny as well as in phylogeny; they represent therefore secondary gonoducts.

The *cœlomic cilia* (Fig. 1, A, B) are represented as long ciliary rows; they occur in the trunk and in the parapodial cavities and also in the cavities of the cirri and of the head tentacles. The cœlomic epithelial layer is so thin that no cell boundaries are present, the nuclei are rare. There is generally one nucleus in the neighbourhood of each ciliary row.* The ciliary rows are arranged transverse to the longitudinal axis of the trunk and of the parapodia respectively. In the parapodia they occur on the opposite sides ventral and dorsal, but the first a little approximated to the posterior wall and the second to the anterior wall. The number of both sets is almost equal and mostly 4 to 6. In the trunk region the ciliary rows are more numerous on the ventral side; they are restricted to the interparapodial regions of the trunk and their number is usually 4 to 6. In the caudal region they are much more numerous, about 6 to 10, and are situated closely one behind the other.

The direction of the effective beat is the same in all the cilia of one row and it is also the same in all rows of one side. On the opposite sides (ventral and dorsal) the direction is opposite. The result of this antagonism is that the current of the cœlomic fluid is of a circulatory nature.

The *current* of the cœlomic fluid (Fig. 1, C) runs forward on the ventral side of the trunk, on the dorsal side backwards; in the parapodia it runs on the dorsal side outwards, on the ventral side inwards. The circulation of the parapodia is not confined to the same segment, but the greater part of the fluid which arrives ventrally in the base of the parapodium *enters*

* This can be made out with Fischer's solution of tannin-ferrous sulphate-alcohol fuchsin; it is necessary to let it act directly on the free cœlomic surface.

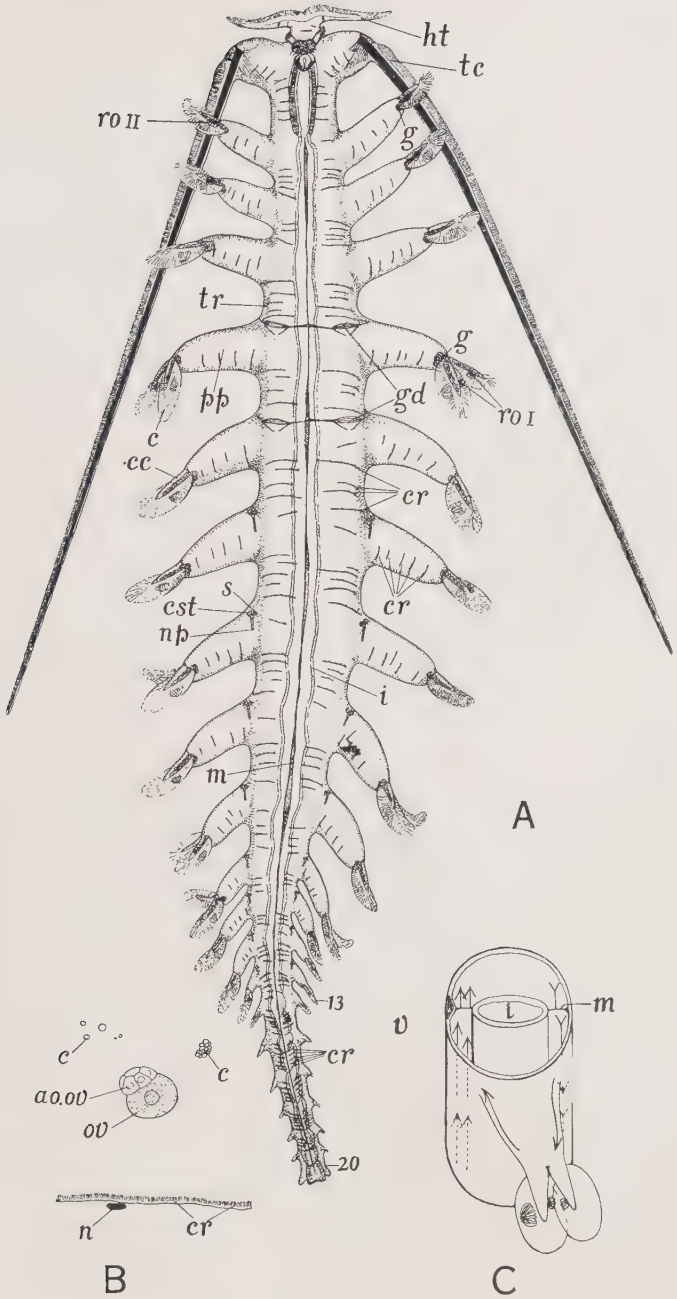

Fig. 1.—*Tomopteris helgolandica* ♀. (Watson Obj. 1, Oc. 2, working table. Reduced to one-half.) ht, head tentacles. tc, tentacular cirri (with a bristle). roI, rosette-like organs (phosphorescent) of first category (hyalin glands). roII, rosette-like organs (phosphorescent) of second category (rosettes). g, gonad. c, cirrus (=fin). cc, cirrus cavity. s, solenocytes. cst, cœlomostome. np, nephridiopore. gd, secondary gonoducts. cr, ciliary rows. i, intestine. m, mesentery. tr, trunk. pp, parapodium.

B, Content of the cœlomic fluid and ciliary row of *T. helgolandica* (Watson Obj. 3, Oc. 2, working table. Reduced to one-half.) c, corpuscles resulting from the abortive oocytes and also from the secretion of the rosette-like organs. ao. ov, abortive oocytes. ov, growing oocyte. cr, ciliary row with nucleus n.

C, scheme of the currents of the cœlomic fluid in *T. helgolandica* indicated by arrows. v, ventral. i, intestine. m, mesentery.

the trunk, and on the dorsal side fluid becomes drawn out from the trunk into the parapodium.

The directions of the circulation are more clear immediately above the ciliated surfaces than in the intermediate region, where the movement is slow and in its direction not constant, owing to the distance from the cilia and the viscosity of the fluid.

The cœlomic cilia in *T. helgolandica* are already present in young stages of nine parapodial segments* and the number of ciliary rows is almost fully established; but there also exists a small increase in the number during the progress of development and sexual maturity.

If we try to judge the general biological significance of cœlomic cilia and of the circulation produced by them we arrive at the following conclusions: (1) the cœlomic epithelium is phylogenetically of entero-cœlic (gono-cœlic) nature and therefore contains the possibility of development of cilia by inheritance from the cœlenteric ancestors; (2) cœlomic cilia are of œcological value especially in those animals where the blood-vessels are wanting and their functions are replaced by the cœlom; (3) the appearance of cœlomic cilia during individual life is not without connection with the development of the sexual products, and there exists also a relation of cœlomic cilia to the system of segmental organs which is clearly expressed in the addition of secondary components (secondary cœlomostomes and gonoducts) to the segmental organs; (4) the question whether in the primitive Annelid-ancestor circulation was carried out by cœlomic cilia or by true blood-vessels is not decided; until this question is solved from other arguments it remains undecided whether the occurrence of cœlomic cilia in the Annelids is a primitive (palingenetic) character or cenogenetic. From the physiological point of view it seems rather clear, that the occurrence of circulation by means of cœlomic cilia is more " primitive " than by means of contractile blood-vessels.

* These stages are still provided with a pair of bristle-bearing appendages (in front of the tentacular cirri) which are usually lost later.

Observations on *Patella vulgata*. Part III. Habitat and Habits.

By

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With 2 Figures in the Text.

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Introduction.

The present contribution continues the account of studies on the common limpet, *Patella vulgata* (**1**, **2**), and forms an introduction to investigations on facts and causes of variation in shell-height, which are being continued and will be published later, and not as Part III of the series as originally intended. The cause of the variation in the shape of the shell in *P. vulgata* (**3**, **6**) has been—and continues to be—a subject of much interest to naturalists. There can be little doubt that the height of the shell varies at least roughly—but not in any simple manner—in correlation with the habitat (**5**), and that as the individual limpet rarely moves many feet away from its point of fixation (**6**, **7**, **8**, **9**) there must presumably be a close relation between certain factors in the habitat and the coexisting shape of the shell. It is therefore important in this regard to review the habits and to note and define carefully the habitats of this animal on the shore.

P. vulgata occurs on the Atlantic shores of Europe (**10**) between tide-marks. On the coasts of Devon and Cornwall the species (excluding for the present the doubtful species or variety, *athletica*) occurs mainly between a level about mean low water and one a little below the high-water spring-tide mark in the habitats and with the congeners shown in Table I, page 278.

TABLE I.

Inter-tidal Habitats of *Patella vulgata* L., and of some associated Organisms in the Plymouth District.

Splash-lines.	Height of tide in feet above or below Datum.		Patella habitats.	Littorina habitats.	Barnacle habitats.	Some Algal habitats.
	17—					(A sp. of Lichen)
	16—			*Littorina neritoides*		Enteromorpha[1]
		15·7 M.H-W.S.	Patella rare	L. *rudis* rare		
	15—					Enteromorpha[1]
					Chthamalus rare	*Pelvetia canaliculata*
	14—	14·1 M.H-W.	Patella	*L. rudis*		
	13—				*Chthamalus stellatus*	*Fucus platycarpus*
		12·25 M.H-W.N.	Patella	*L. rudis*	*B. balanoides* rare	Enteromorpha
	12—					Ascophyllum
			Patella	*L. obtusata*	*B. balanoides*	*F. vesiculosus*
	11—					
			athletica form	*L. littorea*		*F. serratus*
	10—		in pools			Porphyra
	9—					
		8·15 M.T.L.	Patella	*L. littorea*	*B. balanoides*	*F. serratus*
	7—		*athletica* form in pools			
	6—					
		4·6 M.L-W.N.	Patella	*L. littorea*	*B. balanoides*	*F. serratus*
	4—				*B. perforatus*	
	3—					
		2·39 M.L-W.	Patella	*L. littorea*	*B. perforatus*	*F. serratus*
			Patella rare		*Verruca strœmia*	Gigartina
	1—		*athletica* form on rocks			Chondrus
						Himanthalia
	0—	0·18 M.L-W.S.	*Helcion pellucida* rare	*L. littorea* less common	*V. strœmia*	Laminaria, spp.
	−1—					
	−2—		*H. pellucida*			Laminaria, spp.

Notes to Table I.—The levels of the organisms associated with Patella are liable to vary, especially with the local splash-line, and in localities exposed to strong wave-action and strong sunshine. The data regarding tidal levels are for Devonport (see **11**, p. 370) :—

M.H-W.S.=mean high water spring tides.
M.H-W.=mean high water.
M.H-W.N.=mean high-water neap tides.
M.T.L.=mean tide level.
M.L-W.N.=mean low-water neap tides.
M.L-W.=mean low water.
M.L-W.S.=mean low-water spring tides.

[1] Where fresh water occurs.

The Distribution of *Patella vulgata* on a Cliff-bound, Sun-baked Shore.

In studying the distribution of *P. vulgata* on the shore, it was found that at levels above high-water neaps, exposure to direct sunlight is a very important limiting factor. This effect of sunlight is easily observed by taking a rowing-boat at about the time of high water on a neap tide along a rocky or cliff-bound shore which faces mostly, or in parts, in a southerly direction. On the parts of the cliff exposed directly to the sun's rays it is seen that the limpets are distributed along and below the

line *and splash-line* of high-water neaps. Where the water at H.W. neaps runs up angular depressions in the face of the rocks, limpets may be so thick as to outline the splash of the waves (herein denoted as the splash-line*) above the general mean high-water neap level, whereas elsewhere on the dry sun-baked area above this level limpets are absent or rare. Where the cliffs jut out so as to produce shade, or in caves, or on the shaded sides of rocks, limpets will be found above the level of H.W. neaps; that is, in most places where continuous direct sunlight can be avoided. Such is the distribution of limpets on the Wembury shore at the mouth of the River Yealm, near Plymouth, as seen in a calm sea on July 11th, 1928, at high water at 12.40 p.m. (S.T.), when the height of the predicted tide (**11**, p. 3) was 12 feet 7 inches above datum (mean high-water neaps at Devonport being 12·25 feet above datum, **11**, Part I, p. 344). The distribution of limpets on the cliffs near Perranporth, on the North Cornwall coast, shows similar limitations. The cliffs to the south of Perran sands face north to north-west and are sheltered from the sun during the greater part of the day, and are also in many places damp even on a summer day. On these cliffs limpets occur abundantly in most situations above high-water neaps, but on the northern part of the sands the cliffs face westerly and in 1928 were devoid of limpets above high-water neaps except for occasional small individuals hiding under the high-level seaweeds, Pelvetia, and a species of Fucus, probably *platycarpus*, which was zoning above *Ascophyllum nodosum*. On rocky shores which do not face south and yet receive a moderate amount of direct sunlight limpets may extend above high-water neaps, but in such cases they do not usually attain a large size unless they are living in a situation which is in some way maintained in a damp condition, e.g. proximity to a seepage of water. On most north-facing rocky shores—like that of Perranporth—it would appear that limpets are seldom absent above high-water neaps unless the shore be liable to be pounded with gravel or sand, or there is some other obvious deterrent.

Thus the distribution of the limpet on the shore indicates that although this animal can exist in localities which receive a certain amount of direct insolation, there is a limit beyond which existence cannot be maintained, whether the limiting cause be absence of food or direct insolation.

In the south-west of England where the low water of spring tides occurs round about midday (and midnight) (see Fig. 1, p. 281) limpets do not occur in dry places above high-water neaps which are exposed to direct sunlight during the whole, or a large portion, of the daily period

* The splash-line is important at all tidal levels on sloping rocks or sloping beaches in apparently raising the level of a zone. I have seen Patella at least 6 feet above the general high-water spring-tide level in a cave at New Train Bay, N. Cornwall, where existence was made possible by the splash of the waves.

of duration of sunlight; but in more northern latitudes and other localities limpets may be able to exist on the southern faces of cliffs to a greater extent, especially in those situations where the *high water* of the spring tides occurs (see Fig. 2, p. 281) round about midday, e.g. south-east of England and neighbouring Continental coast, parts of northern Scotland, as at Invergordon (see Admiralty Tide-Tables, **11**, *passim*). In considering the habitats and habits of the common limpet, it is certain that the geographical orientation of the rocks comprising the habitat, the latitude of the locality, and the epoch of the day when the limpets are exposed during the spring tides, are all important factors, which if not considered might give rise to great confusion, but which when carefully noted may render concordant many apparent inconsistencies and many apparently opposed statements.

Fig. 1. Conspectus of the tidal changes in the Devon and Cornwall area, shown by a semi-diagrammatic chart of the semi-diurnal tides during a semi-lunar cycle. The time and duration of the exposure of the foreshore at different levels is also shown approximately.

(Data from Admiralty Tide-Tables, Part 1, 1929, from which are plotted the predicted times and heights (in feet) for high and low water for the tides at Devonport from April 7th to April 22nd).

Each small circle denotes the height and time of the tide at low or high water on the date given by the small figure adjacent to the circle. The courses of representative tides only are plotted: (after **11**, II, Table 4), e.g.:—the spring tide on April 12th (thick-line curve); the neap tide on April 18th (thin-line curve), and two intermediate tides on April 8th and 15th respectively (broken-line curves). The large circles give the seasonal maximum and minimum possible daily range of sunshine. The references to different tidal levels, M.H-W.S., etc. have the same meaning as in Table I, p. 278.

M.H-W. (=mean high water) and M.L-W. (=mean low water) occur midway between M.H-W.S. and M.H-W.N., and M.L-W.N. and M.L-W.S. respectively. These are important biological levels, but are not given in Admiralty Tide-Tables.

The heights of high or low water—with reference to the chart datum (which is only 0·18 foot above mean low-water springs)—are plotted as ordinates in feet, while times of day (G.M.T.) at which high or low water occurs are plotted as abscissæ. The cycle of tides shown in the diagram is repeated at essentially the same times and with slight modification in height throughout the year. Around the period of the equinoxes, March and September, the rise of tide during spring tides is higher and the fall lower than at other times: in winter, the morning high spring tides are higher and the succeeding low tides lower than the night tides, whilst the contrary is the case in summer. In the lunar cycle the greater spring tides occur after full moon in winter, but after new moon in summer. With reference to mean tide-level, in this district neap tides rise on the average higher than they fall, but spring tides fall lower than they rise on the average.

The time of high water on the same day varies slightly in Devon and Cornwall, being about one hour earlier in the extreme west (Land's End) than at Devonport, decreasing along the south coast to Devonport,

FIG. 1. DEVONPORT

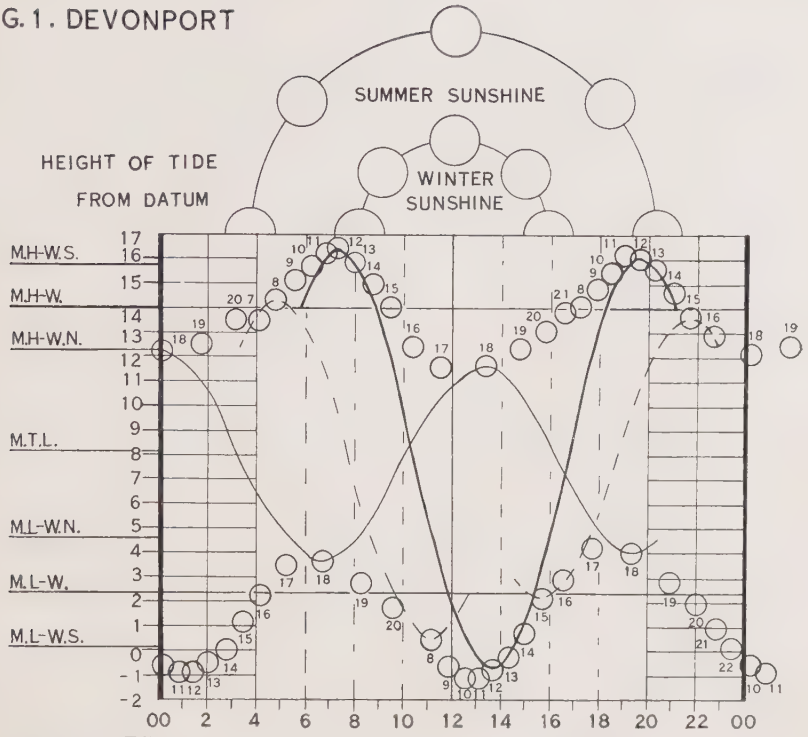
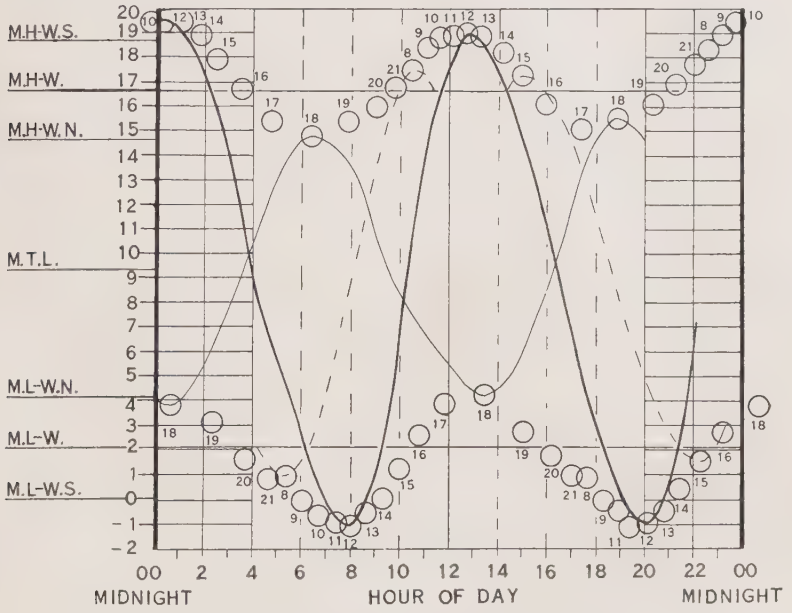


FIG. 2. DOVER



NOTE.—Height of tide from datum is given in feet.

whence it increases to 35 minutes later at Exmouth; it decreases similarly from Land's End along the North Cornwall coast to about 2 minutes earlier at Ilfracombe than at Devonport. (**11**, II, pp. 32 and 54.)

The chart shows that in the Devon and Cornwall area :—

(1) The region on the shore *above* mean high-water neaps (M.H-W.N.) is uncovered by the tide during the greater part of the middle of the day (and middle of the night) during *every* day of the year.

(2) The region on the shore below M.H-W.N. is uncovered by the sea during spring tides, but covered during neap tides, in the *middle* part of the day.

(3) During neap tides the region above M.H-W.N. may remain entirely dry for one or more tides, or in summer, for one or more days, while that below M.L-W.N. may remain covered during one or more tides or days.

(4) The region above mean high water (M.H-W.) may not be covered by the sea during about 7 days and that below mean low water (M. L-W.) may remain covered by the sea during about 7 days in a semi-lunar cycle.

(5) The time of immersion in sea-water of a region above mean high water varies from about 3 hours at spring tides to a slight wetting according to the height of the tide on any day and the height of the region above M.H-W.

(6) The time of exposure of a region of the shore below mean low water (M.L-W.) varies from about 3 hours to momentary exposure according to the height of the tide (above or below datum) and the level of the region below M.L-W.

(7) During the period of the higher tides (i.e., those rising to and above M.H-W. and including the spring tides) the different levels on the foreshore are exposed in the middle of the day, approximately and on the average, as follows :—

M.H-W.	11 to $9\frac{1}{2}$	hours	ranging	between	about	5	and	20·30	hrs.
M.H-W.N.	$9\frac{1}{2}$ to $8\frac{1}{4}$	,,	,,	,,	,,	6	,,	19·30	,,
M.T.L.	ca $6\frac{3}{4}$ to $6\frac{1}{2}$	,,	,,	,,	,,	7·30	,,	18·30	,,
M.L-W.N.	ca $4\frac{3}{4}$ to 4	,,	,,	,,	,,	8·30	,,	17·15	,,
M.L-W.	$3\frac{1}{2}$ to 1	,,	,,	,,	,,	9·30	,,	16·0	,,
M.L-W.S.	2 to 0	,,	,,	,,	,,	11·30	,,	15·0	,,

Fig. 2. Semi-diagrammatic chart of the semi-diurnal tides during a semi-lunar cycle showing the times of exposure of the foreshore at different levels during the daytime in localities where high-water spring tides occur about midday, e.g. south-east of England and neighbouring continental coast, and northern Scotland, as at Invergordon.

(From Admiralty Tide Tables, Part I, 1929, from which are plotted the

predicted times and heights of high and low water at Dover from April 8th to April 21st.)

Fig. 2 shows that in any locality where high-water spring tides occur at about midday the high-water foreshore is necessarily protected during the period of the higher tides from direct exposure to air and sunshine during the hottest part of the day. In the period of neap tides the foreshore down to M.L-W.N. is exposed during the middle of the day. The region about mean low-water springs is only exposed to air and sunshine about 6 to 9 a.m. and 6 to 9 p.m., and in general the exposure conditions to extremes of temperature and insolation are much less severe than in such a region as is shown in Fig. 1.

In Fig. 1, page 281, it is shown that in the area of Devon and Cornwall (and similar tidal localities) the region above high-water neap-tide level is always exposed in the middle of the day to the air, and therefore also in certain situations also to the sun's rays. Thus, where limpets are present on the shore below and up to the level of high-water neaps, and also present in shaded places immediately above this level, while at the same time they are absent in the same locality from intermediate areas above high-water neaps which are exposed to direct sunlight, it is manifest that direct sunlight in these situations is in some manner a limiting factor in the distribution. Since, however, the limpet can exist above high-water neaps in places subject to a certain amount of direct insolation, it is also clear that this animal may be able to exist above high-water neaps at different levels on different shores, according to the duration and intensity of the incident direct insolation in different areas.

The distribution of limpets above high-water neaps indeed shows that individuals can withstand strong direct insolation for a short period, and a less strong direct insolation for a longer period, and also that resistance varies to some extent with the size of the animal (when thickness of the shell is doubtless an important factor). The absence of limpets from strongly insolated areas above high-water neaps may, however, be due either to absence of encrusting (e.g. algal) food, or to the direct effect on the animal of the sun's rays, or both of these factors. In this regard the occurrence of abundance of limpets on the high-water neap-tide line and their absence above this level in a strongly insolated area indicates that the higher level is untenable as a habitat, and that prolonged direct insolation may be as effective a limiting cause as absence of encrusting algal food. Such food is, however, apparently absent from many (shaded) situations at high water where limpets are abundant and apparently flourishing (**8**, **10**, and self), and apart from the possibility of the limpets making long feeding excursions when covered by the tide the mode of feeding in such habitats is not known. There are indeed grounds for suspecting that Patella may obtain food in other ways than in browsing on rocks. This

animal will eat calcareous sand and detritus (H.-W. Looe Is.), and in aquaria I have known it eat putty and red lead, as shown by the fæces, but I have not yet detected any method of feeding whereby plankton is utilised as food. Thus the absence of encrusting algal food in any area cannot at present be regarded in itself as a certain limitation of such a habitat for the limpet.

The spat of limpets—ranging in length from 2 to 8 mm.—have been specially searched for above and below high-water neaps, but even in the latter zone tiny individuals of this size are rarely found except in very damp places, e.g. crevices or small pools. If therefore such spat settled in very dry sunny places, it is fairly certain that they would die from desiccation before succumbing to starvation. Thus, in accounting for the absence of adult limpets in strongly insolated areas of the shore above high-water neaps, it is necessary to allow some value to the fact of relative scarcity of encrusting food, though the direct effect on the animal of the actual intensity and duration of direct sunlight would appear to be the main limiting factor.

The Movements of Patella in Relation to Habitat and Climatic Conditions.

Russell (**5**, p. 856) has shown that there is no agreement among the many observers on the time that the limpet leaves its home in search of food; for example, "Lukis, Jeffreys, and Robertson state that the limpet wanders when covered by the tide; Davis and Fischer that it wanders while uncovered, and Fischer that young ones wander only when covered; Bouchard-Chanteraux that it makes excursions just after the tide goes out; Lloyd Morgan that it wanders chiefly as the tide leaves it and as the tide returns; Lloyd Morgan and Roberts are of the opinion that it does not move about when submerged." Loppens (**9**) found exposed limpets on the move between Ladram Bay and Sidmouth, but never on the beaches near Exmouth. Russell found in his experiments that limpets above 20 mm. or so in length did not wander when uncovered by the tide, but that smaller ones may wander at any time, and concluded that a habit of fixity becomes established only when the shell has attained a length of 10–15 mm., and that they wander chiefly when covered by the tide. The present writer has seen limpets of all sizes on the move away from their "homes" at high and low-tide levels at some time or other. At high water in damp situations or in situations not exposed to direct sunlight some individuals can usually be found creeping and feeding away from the home, but in dry situations at high water which are exposed to sunlight the animals are rarely seen on the move except in damp or wet weather. Small to medium-sized individuals

may be seen moving on the shaded side of rocks at various tidal levels even in warm sunny weather, as may also large individuals under seaweeds near low-water mark, but limpets are very rarely seen moving when exposed to direct sunlight, while probably everyone can form a mental picture of immobile Patella at or near high-water mark in sunny warm weather.

Thus the factors controlling the feeding movements of the limpet when uncovered by sea-water appear to be mainly those which contribute to the risk or absence of risk of desiccation, and there can be no doubt that the main feeding excursions are made in all habitats when the animals are covered by water. By rowing alongside rocks covered with limpets, especially when the tide is rising at about the time of high-water neaps, it is easy in calm weather to see that the animals begin to move away from their scars very soon after immersion, just as Wells found for Acmæa and Lottia (**13**).

It is now a well-established fact that a majority of the medium to large-sized individuals return to a definite position in space after undertaking feeding excursions (see Russell, **5** ; Pieron, **7** ; Loppens, **9**, and Orton **8**, and **2**) ; but this general statement requires qualification. I agree with Loppens (**9**) that sometimes individuals do not return to the same place, and that evidence of this can sometimes be found in the lines of growth on the shell. Loppens states : " En effet, si la place ne convient plus, soit que la nourriture y manque, soit que la roche s'est trop effritée, ou pour n'importe laquelle raison, le mollusque cherche une autre résidence et ne revient plus à la première. On remarque cependant que beaucoup d'individus résident longtemps à la même place si elle est convenable. Patella peut, en effet, circuler dans un rayon de 2 mètres pour chercher la nourriture et retrouver aisément sa place sur les rochers." It is probable that Patella changes its " home " more often on a smooth and wet surface than on an uneven surface, while at the same time it is undoubtedly true that the bulk of the individuals retain the same scar for long periods in most habitats where the surface of attachment is uneven. On Padstow Dock vertical walls, which have a somewhat rough though uniformly plane surface, I found one limpet six feet above high-water neaps, carrying empty barnacle shells, which had undoubtedly grown below high-water neaps. On such a uniform surface it is probable that a limpet shell will fit fairly well at many places, and the necessity for homing is not so imperative as on more uneven surfaces. Lloyd Morgan's experiments (**12**) also show that a change of site is possible under natural conditions.

In some high-water situations adult individuals occur where younger ones could apparently not exist ; for in such situations small individuals (less than 25 mm.) can only be found in crevices or under weeds (*Pelvetia canaliculata* and *Fucus platycarpus*) where some protection from direct

solar rays and drought is obtained. In these habitats, therefore, the older individuals must have moved into their final positions after attaining a medium size. In a broad consideration of the movements of Patella, it is manifest that the bulk of the larger individuals retain a definite position or home for long periods, and that the changing of the site is unusual for medium to large individuals in most habitats, but may occur more frequently in others, e.g., on smooth and wet surfaces.

The foregoing studies have therefore shown that the period of exposure of the foreshore to direct solar rays, and other conditions conducive to desiccation, as well as relative dampness of a locality, are all very important factors in determining the viable habitats and habits of the common limpet.

Remarks on the form *Patella athletica* F. and H., or *P. vulgata*, var. *depressa* Jeffreys.

The experienced conchologists Forbes and Hanley (**10**) arrived at the conclusion, apparently however with some doubt, that the form *athletica* is sufficiently distinct from other varieties of limpets to be entitled to specific distinction. A little later Jeffreys (**3**), also an experienced conchologist, reduced the status of this form to that of a variety of the common limpet, *Patella vulgata* L., as var. 4, *depressa*. In referring to this form, Jeffreys states : " I once considered myself an adept at picking out the variety *depressa* (or ' China limpet,' as it has been called), by merely seeing the outside ; but I have since failed, and a recent examination and comparison of a great many living individuals of each form has quite convinced me that they are not separate species." In most accounts of the habitat it is stated that the form *athletica* occurs at low water ; for example, Clark, quoted in Forbes and Hanley, states : " They inhabit different levels, the *vulgata* being always in the higher zone." This latter statement is not quite accurate, the form *athletica* occurs in permanent pools (**1**, p. 860) at all levels up to high-water neaps, but also out of pools at low-water mark in some localities on the Devon and Cornwall coast and elsewhere. It has also been shown that the proportion of females with green gonads in this form was greater (in one sample) than in adjacent typical *vulgata*, nevertheless brown and green gonads occur among the females in both types (*loc. cit.*). The range of variation in all the characters of *P. vulgata* is, however, very great ; Jeffreys records that Spence Bate found the lingual ribbon broader and shorter, and the teeth perhaps somewhat larger in *athletica* (≡*depressa*) than in the common type, but the main differences so far found between these forms occur (1) in the habitat, and (2) the nature of the internal calcareous lining of the shell. With regard to habitat the form *athletica* is continuously or

almost continuously immersed in water in contrast with *vulgata*, which experiences in most situations relatively long periods of exposure to the air. The lining of the shell in the former is white and entirely porcellanous, with often an orange coloration in the spatula or apical region, whi'e *vulgata* has a greyish brown nacreous lining with a chalky-white or vitreous greyish white spatula, which may attain a great thickness (e.g., 10·1 mm.) in some high-water habitats.

The correlation between habitat and the quality of the lining of the shell suggests that the shell-differences observed may be physiological, that is, due to the nature of the environment, and therefore not genetic, i.e., specific. Thus it is possible that young limpets developing entirely in pools, or under water, may deposit porcellanous nacreous material on the inside of the shell, while others *of the same brood* developing on rocks exposed to air and light may deposit greyish brown nacreous material and a chalky or vitreous thickening at the apex of the shell. Until this problem is solved, or until some other distinct differential specific character is found in *athletica*, it would seem that there is insufficient ground for regarding the form *athletica* other than a variety of *P. vulgata* L.

At a recent meeting of the Challenger Society with Representatives of British Marine Laboratories, G. C. Robson, who has paid much attention to *P. athletica* F. and H., suggested that this form in its relation to types of *P. vulgata* would provide excellent material for a study in evolution. It is hoped that the foregoing observations may form a nucleus in the development of such a study.

SUMMARY.

The inter-tidal habitats of the common limpet, *Patella vulgata* L,, have been investigated in relation to constant lunar tidal levels and tidal zones. The habitats of some common shore organisms which occur at approximately definite tidal levels or zones—and can therefore be used with discretion for zoning the habitats of Patella—are shown in a chart.

A study of the distribution of the common limpet on the shores of Devon and Cornwall has shown that limpets are absent or rare on those parts of the foreshore above high-water neaps which are subjected to prolonged periods of direct insolation. In the same locality limpets may be totally absent from the high-water region on cliff-faces or rocks facing southerly, but present on adjacent ones facing northerly or north-westerly. Strongly insolated habitats appear to be unviable as a result of the direct effect of the insolation on the animal, but the apparent deficiency of food in such habitats is probably also a limiting factor of importance.

The importance of the *splash-line* of any tidal level is emphasised. It is shown that in Devon and Cornwall the occurrence of *low-water* spring tides at about midday (and midnight) results in exposing to strong sunshine (and correlated factors) those regions of the shore above high-water

neaps which face in a southerly direction. In other localities where *high-water* spring tides occur about midday, equivalent regions of the foreshore are not so strongly nor so persistently insolated as in the former.

Viable habitats may therefore occur in different regions on the shore in different localities or at different latitudes according to the local orientation of the substratum and local tidal phenomena.

The tendency of the common limpet to wander when uncovered by the tide was found to be greatly influenced by those factors in the environment which do or do not incur risk of the animal being dried up. Wandering may occur at any level of the exposed shore in damp or shaded environments, but rarely at any level in the absence of protection from strong sunshine, hence many apparently conflicting statements on this subject may be reconciled. It is considered that the main feeding excursions or operations occur in all habitats when the animal is covered by the tide. It is shown that the habits and viable habitats of the common limpet are determined in a significant manner by factors representing the period of exposure of the foreshore to direct solar rays, other conditions conducive to desiccation, and the relative dampness to the environment. The characters of the doubtful species, *P. athletica* F. and H., are discussed briefly. It is noticed that this form differs from *vulgata* mainly in habitat and the quality of the lining of the shell, and it is suggested that the shell-quality may be a particular physiological product resulting from the special environment, and not to a genetic—and specific—factor.

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On the Occurrence of *Echinus esculentus* on the Foreshore in the British Isles.

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Records and Significance of Occurrence on the Foreshore.

Echinus esculentus, the larger common sea-urchin, occurs in the British Isles between tide-marks on rocky shores at about low-water spring-tide level in the localities given in Table I, page 292. It is, however, absent from apparently suitable foreshores in the Plymouth district, for reasons which are discussed in the present paper. Chadwick (**1**) states that "In Port Erin Bay it may be collected by hand on the beach, and on the ruined breakwater at low water of spring tides." Elmhirst (**2**) records that "In this district (Millport) *E. esculentus* occurs abundantly between tide-marks in spring and early summer on rocky coasts; a few may be found at almost any other season. About February or early March a shoreward migration seems to set in, so that in suitable weather conditions some hundreds may be collected at springs between April and June. Then their abundance decreases until about November, from when until January it is at a minimum."

Storrow (**3**) reports that these "sea-urchins were plentiful on the local rocks (at Cullercoats, Northumberland) during July of last year (1920)," and it is known that *E. esculentus* is collected at low water by the Leeds University Biology Classes at Robin Hood's Bay, Yorkshire. Miss Trewavas (**4**) collected 5 specimens of *E. esculentus* near low-water mark during two equinoctial spring tides at Mousehole and an adjacent island on the south Cornwall coast, and states that "It should be mentioned that both these shores are sheltered on the west by the mainland, while the island acts as a breakwater on the east. This sheltered position

may be connected with the occurrence of *E. esculentus* above low-tide mark in this locality," and further suggests that " either the climatic conditions of Cornwall or the Cornish seas, as contrasted with those of the Isle of Man, are unsuitable to the occurrence of ' zarts ' (*E. esculentus*) in the tidal zone ; or the general climatic conditions are suitable and, except in the case of Mousehole, local conditions are unfavourable." In this locality the fishermen report that " zarts " are often found exposed at low water, but elsewhere in Devon and Cornwall no records of the occurrence of the larger common sea-urchin on the foreshore are known, except a reference by Cocks (**5**) in 1849 to the finding of a young specimen of *E. sphæra* (almost certainly=*E. esculentus*) attached to stones at low-water mark in the Falmouth locality.

E. esculentus does not occur on the well-known rocky foreshores in the Plymouth district (**6**), and I have not seen it on rocky shores at low-water spring tides in frequent visits to Looe mainland and Island at all times of the year ; in occasional visits to the Falmouth district (July) ; to Gribben Head (Sept.) ; to Widemouth Bay, Bude (April and Sept.) ; to Crackington Haven (Sept.) ; to Croyde Bay (Oct.) ; to Morwenstow (Marsland, Sept.). Nor did I find it at Sennen Cove (April), where the fishermen report that large " sea-eggs " (*E. esculentus*) may sometimes be obtained from a boat at low-water spring tides. At all these localities, however, *Parechinus miliaris* (=*Echinus*) were discovered hiding under stones or in crevices.

E. esculentus probably occurs on rocky foreshores in other less well-known localities, especially in Scotland and Ireland, and Dr. Marie V. Lebour informs me that she collected when a schoolgirl large sea-urchins —almost certainly *E. esculentus*—at Kyle Akin, in the Isle of Skye, Scotland. The absence of the species from apparently suitable and much-worked rocky shores in the Plymouth district, and in Devon and Cornwall generally, is noteworthy, and challenges explanation.

Offshore it is known (**7**) that *E. esculentus* occurs all around the British Isles down to depths of about 50 fathoms usually, but sometimes also in deeper water.

The fact that *E. esculentus* occurs off the coast all around the British Isles renders it virtually certain that the post-larval stages will be washed on to most shores from off-shore situations at some time, and would establish themselves in any localities where conditions were favourable. In the Plymouth district this species occurs in 5 to 10 fathoms close in-shore (e.g. off the Mewstone and Revelstoke Point) and has never been recorded (except as flotsam) on the adjacent rocky collecting-grounds in this locality. The existence of adult individuals so close to the shore on this part of the Devon coast makes it highly probable that the post-larvæ will be fairly frequently cast on the shore, as indeed are those of *P. miliaris*.

It is therefore a reasonable inference that the post-larvæ and the young of *E. esculentus* cannot exist on the foreshore in this locality. In a similar way it may be deduced that the general conditions are unfavourable on other rocky shores, which are apparently suitable habitats, but are constantly devoid of this sea-urchin. The general distribution of *E. esculentus*, however, indicates that this Echinoid is essentially a demersal form. Its occurrence on the foreshore may be regarded, therefore, as due either to highly favourable local conditions, which may produce a habitat suitable for both adults and young during the greater part of the year, or the habitat may only be suitable for a temporary shoreward migration at a certain part of the year. The sporadic occurrence of *E. esculentus* on the shore on some parts of the coast (**3**) indicates that this species tends to migrate shorewards, as Elmhirst noticed at Millport (**2**), at certain seasons.

Discussion on some Factors Determining Foreshore Distribution.

In reviewing the localities where *E. esculentus* occurs on the shore it would appear that some fundamental difference occurs in the general environmental conditions at Plymouth in comparison with those especially at Millport and Port Erin, for in the former locality occur protected rocky shores apparently suitable for but devoid of *E. esculentus*, and in the two latter *E. esculentus* thrives in the region of ordinary low-water springs.

In a comparison of the general conditions in the localities in the British Isles where this sea-urchin does and does not occur in apparently suitable habitats above low-water springs, one broad correlation of importance may be discerned, namely, connected with the time of day of low-water spring tides, but this requires to be considered in relation to other factors.

The chief factors contributing to the presence or absence of *E. esculentus* on the shore appear to be :—

1. The periods of the day when low-water spring tides occur.
2. The latitude of the locality.
3. The nature of the foreshore and its degree of exposure to wave-action.
4. The general seasonal hydrographic conditions in the locality.
5. The nature of the substratal approach to the foreshore from deeper water.

Time of Low-water Spring Tides.

It has been shown in a preceding paper in this *Journal* (**8**, p. 277, herein) that low-water spring tides occur on the Devon and Cornish coasts at about and just after 1 a.m. and 1 p.m. (**8**, Fig. 1, p. 281). As a result of this local tidal phenomenon the region about low-water spring-tide level is

exposed to air and sunshine in nearly the hottest part of the day, and to air in a very cold part of the night. On the other hand, at Millport and Port Erin, low waters in the spring tides occur in the early morning and in the late afternoon or early evening at about the same times as at Dover (see **8**, Fig. 2, p. 281). There is thus a marked difference in the temperature conditions on the shore at the time of low water at Plymouth as against those either at Millport or Port Erin, and these differences will be accentuated by the difference in latitude.

The variation in the time of high-water spring tides on the coasts of the British Isles is especially well shown in a figure by Jenkins (**9**, Fig. 21, p. 126), while the actual (predicted) times of high and low water in particular localities are given in Admiralty Tide Tables (**10**), Parts I and II. The standard high and low tides in any locality are those which occur immediately after the moon, at full or at the change (i.e. new), has crossed the meridian (H.W. F. and C. and L.W. F. and C.), but these are not the highest or the lowest tides. The highest and lowest tides occur one to two hours later in the day than those immediately following the full and the change of the moon (see **11**, Figs. 41–43, and **8**, Figs. 1 and 2). Thus at Devonport the time of H.W. F. and C. is 5.32 (**10**, II, p. 32), but the highest tides occur about, i.e., before and after, 7 a.m. and 7 p.m. (or 19 hours), and the lowest round about 1 hour and 13 hours (see **8**, Fig. 1, p. 281).

The epochs of the day and night, before and after which high- and low-water spring tides occur in the various localities where *E. esculentus* is found on the foreshore —including Kyle Akin—are shown approximately in the following table :—

TABLE I.

Correlation of the Mean Time of Low-water Spring Tides and the Occurrence of *E. esculentus* on the Foreshore.

No.	Locality.	H.W. F. & C.	Approx. mean time of day of H.W. springs.		Approx. mean time of day of L.W. springs.		Lat. N. ° ′	Occurrence of *E. esculentus* on the foreshore.
1.	Plymouth District and N. Cornish Coast (Devonport)	5.32	7.0	19.0	1.15	13.15	50 22	Absent.
2.	Mousehole (Penzance)	4.35	6.0	18.0	0.15	12.15	50 07	Occasional at L.W. equin. springs.
3.	Robin Hood's Bay (and Cullercoats) (Whitby)	3.45	5.15	17.15	11.30	23.30	54 29	Present ca. L.W. equin. springs.
4.	Isle of Man (S.) (Port St. Mary)	11.10	0.40	12.40	7.0	19.0	54 04	Present L.W. ord. springs.
5.	Millport, Scotland	11.50	1.20	13.20	6.30*	18.30	55 45	Ditto.
6.	Kyle Akin, Isle of Skye	6.16	7.45	19.45	2.0	14.0	57 16	Ditto.†

* The interval between H.W. and L.W. springs varies from 5¼ to 5½ hours at the Standard port, Greenock.

† Dr. Lebour's record from memory, see p. 290.

A review of Table I shows that where *E. esculentus* is easily obtained at low water on ordinary spring tides, localities 4 and 5, the time of low water falls in the early morning and late afternoon. If, however, Kyle Akin proves to be a locality where the sea-urchins are also normally easily obtained, it is seen that the time of low water in this locality is, on the contrary, in the hottest part of the day, and approaching the coldest part of the night. In locality 3, where *E. esculentus* occurs low in the zone, the time of low water is very nearly midday and midnight, while in locality 2, where sea-urchins only occur at dead low-water springs, and not in abundance, the time of low-water springs is just after midday and midnight. At Plymouth, and in North Cornwall, where *E. esculentus* is absent, low-water falls about 1.15 in the night time and 1.15 in the early afternoon.

There is thus a broad correlation at the lower latitudes between the occurrence of low-water spring tides in the morning and evening and the presence of *E. esculentus* on the shore at the level of low-water ordinary spring tides; and the absence of the sea-urchin—or its occurrence at a very low level on the foreshore—when low-water spring tides fall about midday and midnight. It would appear that at the lower latitudes at Mousehole and Robin Hood's Bay tidal and climatic conditions are just sufficiently favourable to permit the existence of *E. esculentus* at extreme low-water mark, but that at the higher latitude at Kyle Akin conditions may be sufficiently favourable to permit the existence of *E. esculentus* when low tides occur at the hottest part of the day.

Nature and Exposure of the Foreshore.

It is a fundamental fact that life on a rocky foreshore is inversely proportional in amount to the degree of exposure of the foreshore to wave-action. Very few freely moving animals can live above low-water mark on a wave-swept beach unless protection can be found under stones or in crevices. Thus even *P. miliaris* is absent or rare on heavily swept beaches where crevices and stones are rare, and it may be assumed that *E. esculentus* would require greater protection on the shore than its smaller ally. To avoid exposure to air and sunshine, the smaller sea-urchin, *P. miliaris*, hides at the time of low water under stones and in remote crevices, but the larger size of *E. esculentus* would only permit this habit on foreshores where large rocks occur, or where gulleys are common. *P. miliaris* has also the habit of covering itself with shells, stones or bits of seaweed, and such a habit undoubtedly gives additional protection from desiccation and extremes of temperature during the time of low water. *E. esculentus* does not adopt this habit in 5 to 10 fathoms of water, and it would be interesting to know whether such a habit is acquired anywhere on the foreshore.

There can be no doubt, therefore, that the large size of *E. esculentus* is an important factor in rendering this species unsuitable for life above low-water mark on any foreshore, and particularly on those where very high or very low temperatures prevail at low water, and where protection is obtained with difficulty from exposure to air, sunshine, and direct wave-action. Most of the localities given in Table I, page 292, are protected in some measure from exposure to heavy seas. Robin Hood's Bay, Cullercoats, and some places on the north Cornish coast, are relatively exposed, but on the exposed coast at Robin Hood's Bay it would appear that the existence of gulleys at about low-water level afford a sufficient measure of protection from wave-action. It is again of interest to note, however, that sheltered localities in the Plymouth district yield no populations of *E. esculentus*.

Hydrographic and other Factors.

If the shoreward movement of *E. esculentus* is a spawning migration, as suggested by Elmhirst (**2**), it is probable that the animals are seeking a region of higher temperatures, such as exists on the shore in spring and summer (**12**). In this event the need for migration may vary in different localities. It is possible, for instance, that sufficiently high temperatures for spawning may occur during a great part of the year below low water in the South of England (as, in fact, is the case), whereas in higher latitudes the required degree of temperature may not occur off-shore until summer-time, but may easily occur over a greater range of—or earlier in—the year in an inshore habitat.

E. esculentus spawns naturally at Plymouth during the period April–June (ripe individuals regularly give successful fertilisations in March in the Plymouth Easter Class), and April–June is the period Elmhirst gives (*loc. cit.*) for the inshore spawning migration at Millport. The sea-temperature off Plymouth rises in this period from about 9·0° to about 13° C. (**12**, Table I), and at Millport, in shallow water, from about 45° to 52° F. (7·22 to 11·11° C.) (**13**). Thus, if a temperature of 10° to 11° C. be required for spawning, it is clear that *E. esculentus* would need to migrate shorewards at Millport in order to obtain the required temperature in spring or early summer. On the exposed foreshore the Echini would be subject to sea and air-temperatures, which in the daytime in spring and early summer would be higher on the average than those of the sea off-shore (**12**, p. 249, with bibliography).

These considerations tend to confirm the observation by Elmhirst that the appearance of numbers of *E. esculentus* on the foreshore at Millport is a result of a spawning migration, on the assumption that the optimum temperature for spawning is a specific character. As a consequence it would appear that in low latitudes (with higher mean sea-temperatures)

there is less reason than in higher ones for *E. esculentus* to migrate to the foreshore for the purpose of spawning.

The general distribution of *E. esculentus* indicates that at moderate depths (15–30 fathoms) this animal does not frequent fine sandy grounds (**14**). Thus the occurrence of a belt of sandy ground between a rocky foreshore and rough ground off-shore might act as a deterrent to migrating *E. esculentus*, for this large short-spined Echinoid would no doubt be subject to the danger of rolling by wave-action when passing over sandy ground in shallow water.

CONCLUSIONS.

It would appear that the presence of *E. esculentus* on a foreshore is dependent upon the following combination of factors :—

1. The necessity for finding a spawning-ground where temperature (or correlated factors) is greater (or have higher value) than in the deeper off-shore water at a certain season of the year, which is usually the hydrographic spring.
2. A suitable rocky ground protected from excessive wave-action.
3. A foreshore habitat where exposure at low spring tides does not occur in the hottest part of the day at relatively low latitudes (e.g. 50–51°), and
4. An approach to the shore from off-shore without an intervening belt of fine sand.

There can be little doubt that the incidence of the mean time of day at which high- and low-water spring tides occur has an important bearing on the constitution, distribution, and abundance of the fauna and flora in any particular locality. Therefore the absence of *E. esculentus* from the protected foreshores in the neighbourhood of Plymouth would appear to be due primarily to the absence of any necessity for a spawning migration shorewards at this latitude; and secondarily to the fact that low-water spring tides occur in this locality round about the hottest part of the day and near the coldest part of the night, thus rendering the region at low-water unsuitable for this large Echinoid.

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Photo-electric Measurements of Submarine Illumination throughout the Year.

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With 1 Figure in the Text.

Accounts have been given in previous papers (**1**, **2**, and **3**) of measurements of submarine illumination carried out near Plymouth by means of photo-electric cells. The present paper records the results so obtained during 1928, together with a description of such modifications of the apparatus as further experience had shown to be desirable.

Use of Opal Glass Diffusing Windows

In view of the troublesome and uncertain nature of the obliquity and azimuth corrections for photometers with ground-glass windows (**3**, p. 463), diffusing windows were fitted to all the photometers used on, or after, March 6th, 1928 (Series 24 *et seq.*). These windows consist of thin glass, opalized on both surfaces, supplied by Messrs. James Hetley & Co., 35 Soho Square, London. This is the best material that we have found yet for the purpose, since it is permanent, and does not cut off an undue proportion of the light. Its diffusing properties were found to be so good that the only obliquity factor required is that for reflection losses at the front surface of the glass (**2**, p. 184). Thus, the effect of azimuth may be entirely disregarded, and the same small obliquity correction applied to any photometer when used in air. As will be seen later, the average illumination in the sea seems to be at a rather low angle, about the same as that from a uniform grey sky. The obliquity factor for the water-glass surface at this angle would about compensate for the factor allowing for the reduced reflection loss at a water-glass surface as compared with an air-glass surface. Thus, when the submarine photometer is being standardised by comparison with the deck photometer the readings of both photometers are multiplied by the same

obliquity factor (**2**, p. 184) corresponding to the conditions at the time, but when the submarine photometer is submerged the corresponding factor is taken as unity.

The use of this glass reduced the sensitivity of photometer G to direct light to 47·5% of its former value. Photometer L, being, originally, relatively much less sensitive to oblique light, had its direct light sensitivity reduced to 32·5%. As, however, the opal glass had also the effect of reducing the obliquity factors for low-angle light, slightly for G, and considerably for L, the effect of the glass on either photometer when illuminated by ordinary daylight, was to reduce the reading to about one-half. The advantages of the diffusing surface far outweigh this loss of sensitivity.

The opal glasses were placed in front of the existing photometer windows, the apertures of which they covered with considerable overlap. The opals on the submarine photometers K and L fitted inside the metal rims surrounding the windows, and were attached with a little "Sira" wax. The large window of photometer G was reduced to 5 cm. aperture by a thin metal diaphragm, on the top of which the opal was placed.

With the opal in position and an anode potential of 60 volts, G required 167 metre-candles of perpendicular illumination to pass a current of 10^{-9} ampere.

Preliminary tests on the effect of this opal glass on the colour-sensitivity of the photometers shows that it is not important.

New Photometers.

In September, 1928, the Kunz cell in photometer K was replaced by another potassium hydride argon-filled cell made by the General Electric Co. This is considerably more sensitive than the older type of cell. Moreover, as it was felt that a quite unnecessary factor of safety had been used in designing the windows of the submarine photometers (**1**, p. 104, or **2**, p. 181), the aperture in this photometer was bored out from about 3 to about 5 cm. in diameter, the metal surrounding it being enamelled white.

This photometer is designated J. Its sensitivity on October 12th was 10^{-9} ampere for 0·6 m.c. with anode potential 88 volts. For bright light it is generally used at 3 volts, when its sensitivity, which, like most gas-filled cells is not constant, has been known to vary between 3 and 6 m.c. per 10^{-9} ampere. It is proposed to try a method which has been suggested by the makers for improving the constancy of this cell, by passing a sufficient current through it to cause a glow discharge just before use.

About the same date the deck photometer G was replaced by a photo-

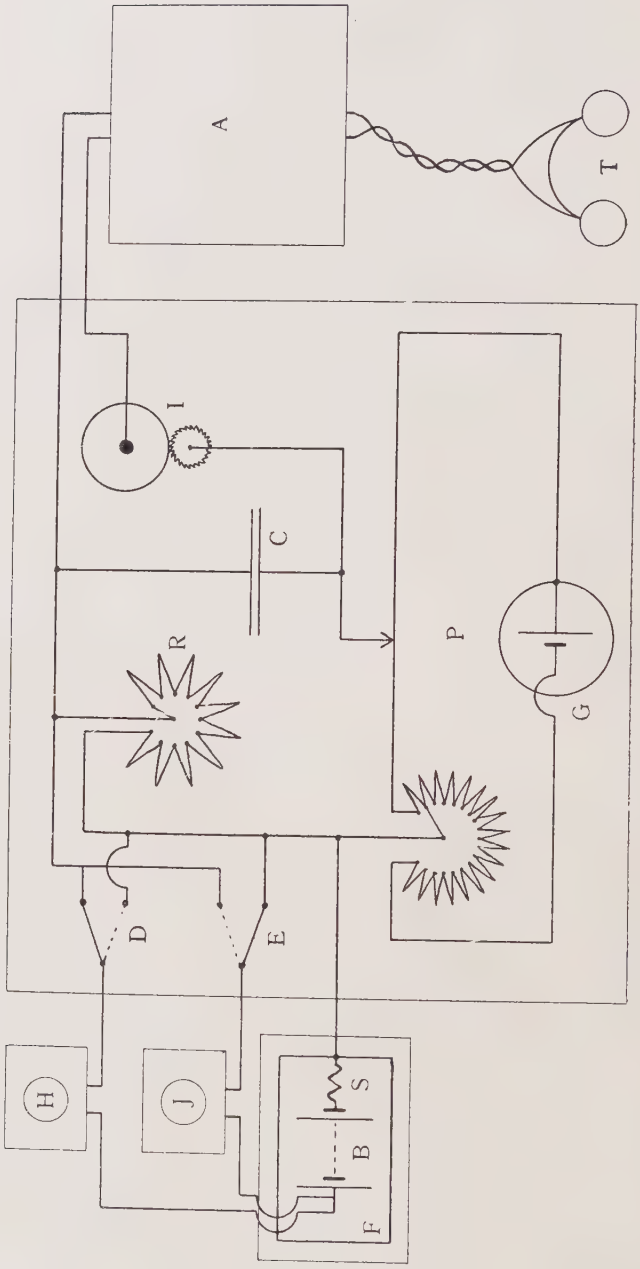
meter, H, containing another vacuum potassium cell which had been in use for some years on shore. This cell had been remounted, and fitted with an opal window instead of the original ground-glass one. It is more than four times as sensitive as G and only requires 40 m.c. to give 10^{-9} ampere with anode potential 60 volts.

Modifications in the Electrical Apparatus.

It was found that, for work in bad weather, the original apparatus suffered from certain grave defects. In the first place, the collection of so many circuits in a single box, which had been arranged to secure compactness, rendered satisfactory insulation more difficult, so that on very damp days "dark currents" became extremely troublesome. Secondly, this box was very heavy, which made the task of landing it from a small boat on the rocks below the Laboratory at Plymouth a difficult and dangerous one if any sea were running. Embarking it was equally difficult, and the use of any other landing-place involved its carriage over a considerable distance. Thirdly, the sound of the telephone was scarcely loud enough for comfort amid the numerous sounds which occur in a small vessel rolling heavily in a seaway, and, finally, the system of connecting the photometer cables alternately to the high-tension battery by means of wander-plugs was unsatisfactory for several reasons.

Accordingly, in October, 1928, the amplifier with its high- and low-tension batteries and also the main high-tension battery were removed from the box. This lightened the latter considerably, and allowed the apparatus remaining in it to be more conveniently arranged. Space was only provided in which one or two aluminium hot-water bottles could be placed if necessary to help in keeping the insulating surfaces dry in damp weather. This is necessary, as leakage currents over the surface of the ebonite potentiometer panel will cause "dark currents" even if the effects of extraneous leakage currents are eliminated by means of guard sheets. The design of the potentiometer is such that it would be very difficult to eliminate these internal leakage currents. For this reason it is better to disconnect the standard cell (which is not shown in the figure) from the potentiometer when taking readings under bad conditions.

The figure shows the general lay-out of the apparatus, as modified. A is the two-valve amplifier, which is of a more powerful type than that previously used. The input terminals are protected from the possibility of surface leakage from the batteries by guard rings of tin-foil gummed to the ebonite panel. It is most important that the telephones, T, should be connected on the negative side of the high-tension battery,


A
T
I
C
R
P
G
D
E
H
J
S
B
F

as otherwise a comparatively large P.D. may occur between the observer and the potentiometer, causing very serious "dark currents."

B is the anode battery, consisting of two 60-volt H.T. dry batteries. This is mounted on rubber insulators inside a metal box, F, which, in turn, is similarly insulated from the wooden box which surrounds and protects the whole. F is connected to the negative pole of the battery through a safety resistance, S, which consists of a bobbin resistance of 9,995 ohms made for a Crompton "All Test" voltmeter. F also carries two insulated terminals, to which the anode cables of the photometers, H and J, are connected. Either of these terminals can be connected by means of a wander-plug to any suitable tapping on B. This arrangement is mechanically much more satisfactory than the direct attachment of the heavy cables to the battery by means of wander-plugs. The effects of leakage currents along the surfaces of the cables are eliminated, as before, by guard wires twisted tightly round the cables and connected to F. These are not shown in the figure.

D and E are two 2-way switches to which the negative leads from H and J are connected. With these in the positions shown in the figure the current through H passes through the 100,000 ohm resistance R, and is measured by the potentiometer P, while that through J flows directly back to F and the negative terminal of B. To measure the current through J it is only necessary to reverse the switches. This arrangement enables successive readings to be taken very quickly, and ensures that the potential is applied to the photometers and cables the whole time, so that soakage effects are eliminated. When readings of a gas-filled photometer have to be taken at two different anode potentials at a given depth, it is better to compare the reading with one potential with the reading of the deck photometer, and then repeat the comparison with the new potential, sufficient time—say, several minutes—having elapsed to prevent errors due to soakage. Well-insulated electric light "corridor" switches are very suitable for use at D and E. They are mounted on an ebonite panel which also carries the terminals to which the cables are connected.

R is generally used at 100,000 ohms, but can be set to any lower multiple of 10,000 ohms which may be convenient for measuring larger currents. The capacity of the mica-insulated condenser C is 1 μF. The interrupter I has already been described (**3**, p. 458).

As the terminals of R are connected to points near the positive end of the potentiometer, the possibility of external leakage from the negative end of the potentiometer battery was eliminated by mounting it on an insulated guard plate G connected to its positive terminal. The standard cell and the amplifier also stand on guard plates (not shown in the figure) which are connected to G.

Results.

The results obtained are shown in Table I, which is a continuation of Table II of our 1928 paper, the various symbols having the same significance. The work was mostly carried out at International Hydrographic Station E1, which is about 10 miles S.W. of the Eddystone lighthouse and about 20 miles from the Plymouth Sound breakwater. As before, the values of the vertical absorption coefficient, λ, for the layer between 0 and 10 m., which are printed opposite the mean depth, 5 m., are marked with an asterisk to show that a surface loss of light of 15% has been assumed. The other values of λ are obtained from the values of the percentage illumination, p, for the levels immediately above and below, respectively. In a few cases the mean of these depths differs somewhat from that opposite to which λ is printed. The vertical illumination is tabulated in thousands of metre candles (k.m.c.).

Series 25 resembles Series 15 in that the photometer window was vertical, so as to measure horizontal light. They differ in the fact that in Series 25 opal glass was used. The effect of this is seen when we compare p_h of Series 25 with the corresponding value of p in Series 24. The ratio p_h/p is given in the last column of Series 25, where it will be seen that its mean value is as high as 0·54, as compared with 0·14 in Series 15–16. The latter value is known to be too low, owing to the small sensitivity of the photometer to oblique light, but the intensity of the horizontal illumination in Series 25 is rather surprising. Too much stress must not be laid on this result, as more than two hours elapsed between the two series, and the water may have been clearer in the later one, although the approximate uniformity of the ratio p_h/p at different depths may be taken as evidence against this.

It is obvious that in air, under a perfectly uniform, sunless sky, the value of H/V would be 0·5, the vertical photometer only receiving light from half a hemisphere. Thus, the results of Series 24 and 25 indicate that the average obliquity of submarine illumination is about the same as that of diffuse daylight in air. The previous results corresponded more closely with the same light after refraction in a smooth-water surface, which would considerably increase its average altitude (**2**, p. 184, table). The average altitude of the submarine light has very little effect on the sensitivity to vertical light of a photometer with a diffusing window, as the effect of obliquity on the small reflection loss at the water-glass surface is negligible. Thus, the values given for V are not affected. On the other hand, the ratio of the total illumination, I, to V would be 2·0 for light of the distribution suggested by Series 24 and 25, as compared with 1·19 for that assumed from the results of Series 15 and 16 (**2**, *loc. cit.*). As the rate of photosynthesis depends on the total illumination, the average altitude of the light is of importance, and further measurements are desirable.

TABLE I.

Date, Remarks, etc.	T G.M.T.	α	Light.	β	d metres	V_a k.m.c.	V k.m.c.	p %	λ
Series 23. 1.3.'28.	1.26 p.m.	31	Bright Sun	4	r	66.5	66.5	100	—
K Photometer. At El.	1.34 ,,	,,	,,	,,	5	66·5	26·1	39·4	0·127*
Wind S.W., light. Long	1.39 ,,	,,	,,	,,	10	66·5	15·7	23·7	0·103
swell, small surface rip-	1.44 ,,	,,	,,	,,	15	66·5	9·6	14·4	0·099
ples. Clear sky. Approx.	1.48 ,,	30	,,	,,	20	65	5·75	8·85	0·103
depth 70 m. (Chart).	1.56 ,,	,,	,,	,,	25	64·5	3·34	5·15	0·101
High water 12.59 p.m.	2.1 ,,	29	,,	3·5	30	65	2·09	3·22	0·094
Secchi disc 14 m. in	2.6 ,,	,,	,,	,,	35	65·5	1·30	2·00	0·101
shadow of ship at 4.30	2.13 ,,	28	,,	,,	40	64	0·75	1·17	0·109
p.m.	2.22 ,,	,,	,,	,,	45	62·5	0·42	0·67	0·127
	2.53 ,,	25	,,	,,	50	61·5	0·200	0·326	0·138
	3.3 ,,	24	,,	,,	55	54	0·090	0·167	0·156
	3.11 ,,	23	,,	3	60	52·5	0·036	0·068	0·198
	3.17 ,,	22	,,	,,	65	50	0·011	0·023	0·144
	3.26 ,,	21	,,	,,	70	48·5	0·008	0·016	—
	3.33 ,,	,,	,,	,,	45	47·5	0·175	0·357	—
	3.57 ,,	19	,,	,,	20	40·5	2·52	6·2	—
	4.8 ,,	17	,,	2·5	5	38·3	10·1	26·4	—
	4.15 ,,	15	,,	2	r	33·8	33·8	100	—
Series 24. 6.3.'28.	12.34 p.m.	34	Bright Sun	3	5	75	30·9	41	0·152*
L Photometer. About	12.39 ,,	,,	,,	,,	10	73·5	13·7	18·6	0·155
1·5 miles N.W. of Eddy-	12.44 ,,	,,	,,	,,	15	73	6·35	8·7	0·151
stone, drifting slowly	12.50 ,,	,,	,,	,,	20	73·5	3·03	4·1	0·147
S.W. Depth 51 m.	12.57 ,,	,,	,,	,,	25	72·5	1·47	2·0	0·155
(Sounding). Wind N.W.,	1.1 ,,	,,	,,	,,	30	72	0·63	0·87	0·152
light. Very little swell,	1.5 ,,	,,	,,	,,	35	71·5	0·31	0·435	—
surface ripples. Sky									
clear. High water 6.20									
p.m. Secchi disc 13·5 m.									
in shadow of ship at 2.40									
p.m., 11·5 m. at 2.50 in									
sun.									
							H	p_h	$\frac{p_h}{p}$
Series 25. 6.3.'28.	3.12 p.m.	24	Weak Sun	1·5	5	18·5	4·65	25·1	0·61
L Photometer with	3.17 ,,	23	,,	,,	10	18·35	1·90	10·3	0·555
window vertical so as to	3.20 ,,	,,	,,	,,	15	19·7	0·90	4·55	0·525
measure horizontal light.	3.31 ,,	22	Brighter	2	20	29·6	0·57	1·92	0·47
Sun through light clouds.	3.35 ,,	21	,,	,,	25	29·6	0·33	1·11	0·555
Other conditions as in									
Series 24.									
							V	p	λ
Series 26. 27.3.'28.	1.33 p.m.	—	Cloudy	1	r	39·3	39·3	100	—
K Photometer. At El.	1.52 ,,	—	Bright	,,	5	52·5	18·0	34·3	0·172
Wind N.W., light. Con-	2.11 ,,	—	,,	,,	10	44	6·65	15·1	0·126
siderable swell. Over-	2.57 ,,	32	Weak Sun	1·5	15	65·5	6·25	9·5	0·117
cast, grey sky. High	3.0 ,,	,,	,,	,,	20	64·5	3·02	4·7	0·145
water 9.59 p.m.	3·3 ,,	31	,,	,,	25	64	1·42	2·22	0·162
	3.6 ,,	,,	,,	,,	30	66·5	0·615	0·925	0·160
	3.30 ,,	28	,,	,,	35	64	0·288	0·45	0·127
	3.42 ,,	26	,,	,,	45	44·5	0·060	0·137	—
Series 27. 5.4.'28.	1.2 p.m.	44	Sun	2	r	67	67	100	—
K Photometer. At El.	1.13 ,,	,,	Weak Sun	1·5	5	52	21·4	41	0·139*
Light breeze S.W. Very	1.20 ,,	,,	,,	,,	10	48	10·2	21·2	0·128
heavy roll at times. Blue	1.32 ,,	43	,,	,,	15	41	4·65	11·3	0·129
sky to E. Heavy clouds	1.38 ,,	,,	Cloudy	1	20	28·9	1·68	5·8	0·144
to W. Light variable.	1.56 ,,	42	,,	,,	25	28·5	0·76	2·66	0·132
High water 6.9 p.m.	2.3 ,,	41	,,	,,	30	32·7	0·505	1·54	0·092
Secchi disc 10 m. in	2.11 ,,	,,	Rain	,,	35	32·6	0·345	1·06	0·103
shadow of ship at 4.15	2.16 ,,	40	Fine, Cloudy	,,	40	37·5	0·206	0·55	0·115
p.m.	2.23 ,,	39	,, ,,	,,	45	40	0·134	0·335	0·108
	2.34 ,,	38	Weak Sun	1·75	50	54	0·104	0·192	0·135
	3.7 ,,	33	Sun	2·5	50	86	0·149	0·173	,,
	3.13 ,,	32	,,	2	55	74·5	0·065	0·087	0·129
	3.19 ,,	,,	,,	,,	60	71	0·036	0·051	—
	3.47 ,,	29	,,	,,	20	66·5	2·83	4·25	—
	3.57 ,,	27	,,	,,	10	60	8·9	14·8	—
	4·5 ,,	26	,,	,,	r	58	58	100	—

Date, Remarks, etc.	T G.M.T.	α	Light.	β	d metres	V_a k.m.c.	V k.m.c.	p %	λ
SERIES 28. 19.4.'28.	11.58 a.m.	51	Bright Sun	4	r	109	109	100	—
K Photometer. At El.	12.8 p.m.	,,	,,	4	a	114	109	95·5	—
Wind N.W., light. Slight	12.21 ,,	,,	Light Cloud	2	5	45·5	22·7	50	0·090*
swell from N.W. Clear	12.31 ,,	,,	,,	,,	10	49	17·2	35·1	0·077
sky with clouds. High	12.40 ,,	,,	Sun	3·5	,,	81	26·7	33·0	0·077
water 5.23 p.m. Secchi	12.50 ,,	,,	Bright Sun	4	,,	121	41	33·8	0·077
disc 18 m. at 4.18 p.m.	12.56 ,,	,,	,,	,,	15	134	29·6	22·1	0·078
	1.49 ,,	48	,,	,,	,,	102	24·6	24·0	0·078
	1.54 ,,	47	,,	,,	20	100	15·6	15·6	0·079
	1.58 ,,	,,	,,	,,	25	100	10·4	10·4	0·075
	2.3 ,,	46	,,	,,	30	99	7·35	7·4	0·088
	2.11 ,,	45	,,	,,	35	97	4·15	4·25	0·119
	2.23 ,,	43	,,	,,	40	94	2·12	2·25	0·121
	2.30 ,,	42	,,	,,	45	94	1·20	1·28	0·114
	2.45 ,,	40	,,	,,	50	89	0·65	0·725	0·115
	3.0 ,,	38	,,	,,	55	84	0·342	0·405	0·109
	3.11 ,,	37	,,	,,	60	79·5	0·192	0·242	0·100
	3.15 ,,	36	,,	,,	65	78·5	0·116	0·148	0·090
	3.19 ,,	35	,,	,,	70	77·5	0·076	0·098	—
	3.35 ,,	34	,,	3·5	45	74	0·73	0·985	—
	3.53 ,,	31	,,	,,	25	73·5	5·8	7·9	—
	3.58 ,,	30	Cloudy	1	,,	25·3	1·77	7·0	—
	4.1 ,,	29	Bright Sun	3	,,	69·5	5·55	8·0	—
	4.8 ,,	28	,,	,,	r	68	68	100	—
SERIES 29. 7.5.'28.	11.13 a.m.	55	Sun	2	r	77	77	100	—
K Photometer. At El.	11.29 ,,	56	,,	,,	a	84·5	76·5	90·5	—
Very light air from N.	11.32 ,,	,,	,,	,,	b	86·5	64·5	74·5	—
Scarcely any swell, sea	11.46 ,,	57	,,	,,	5	85·5	40·5	47·5	0·097*
glassy. Sky hazy with	11.52 ,,	,,	,,	,,	10	85·5	27·6	32·3	0·070
light clouds and hot sun.	11.56 ,,	,,	,,	,,	15	84	19·5	23·2	0·083
High water 7.13 p.m.	12.2 p.m.	,,	,,	,,	20	84·5	12·0	14·2	0·099
Secchi disc 17 m. in	12.14 ,,	,,	,,	,,	25	84·5	7·3	8·65	0·101
shadow on weather side	12.25 ,,	,,	,,	,,	30	83	4·25	5·15	0·099
of ship at 2.58 p.m., 19 m.	12.29 ,,	,,	,,	,,	35	84·5	2·72	3·22	0·104
in sun on lee side of ship	12.35 ,,	,,	,,	,,	40	84	1·53	1·82	0·122
at 3.4 p.m. (V_a=71,000	12.56 ,,	56	,,	,,	45	84	0·80	0·955	0·100
m.c.), 14 m. to windward	12.59 ,,	,,	,,	,,	50	82·5	0·55	0·67	0·091
at 4.0 p.m. and 22 m. to	1.13 ,,	55	,,	,,	55	85	0·327	0·385	0·111
leeward at 4.5 p.m. with	1.21 ,,	,,	,,	,,	60	84	0·185	0·220	0·085
overcast sky (V_a=18,700	1.28 ,,	54	,,	,,	65	85	0·139	0·164	0·060
m.c.).	1.34 ,,	,,	,,	,,	70	84·5	0·102	0·121	—
	1.41 ,,	53	,,	,,	55	81·5	0·277	0·340	—
	1.46 ,,	,,	,,	,,	50	82	0·445	0·54	—
	1.55 ,,	52	,,	,,	40	82	1·42	1·73	—
	2.34 ,,	47	,,	1·5	20	76	10·45	13·8	—
	2.49 ,,	45	Cloudy	1	r	53·5	53·5	100	—
SERIES 30. 13.6.'28.	12.26 p.m.	—	Bright, no Sun	1	r	69·5	69·5	100	—
L Photometer. At El.	12.33 ,,	—	,,	,,	a	61	48·5	79·5	—
Wind S.E., light. Sea	12.40 ,,	—	,,	,,	5	56·5	20·4	36·1	0·133*
smooth with slight swell.	12.45 ,,	—	,,	,,	10	52	11·7	22·5	0·106
Sky overcast. High	12.49 ,,	—	,,	,,	15	52·5	6·55	12·5	0·116
water 1.23 p.m.	12.53 ,,	—	,,	,,	20	53	3·73	7·05	0·114
	12.58 ,,	—	,,	,,	25	46	1·84	4·00	0·141
	1.2 ,,	—	,,	,,	30	41·5	0·71	1·71	0·141
	1.6 ,,	—	,,	,,	35	47	0·46	0·98	0·166
	1.11 ,,	—	,,	,,	37	48·5	0·26	0·535	—
SERIES 31. 13.6.'28.	1.32 p.m.	—	Variable	1	r	34·4	34·4	100	—
K Photometer. Other	1.40 ,,	—	no Sun	,,	5	46	19·9	43·5	0·105*
conditions as in Series 30.	1.47 ,,	—	,,	,,	10	40	11·9	29·7	—
Secchi disc 14 m. at 3.17	2.9 ,,	—	,,	,,	30	48·5	1·77	3·65	0·106
p.m. in lee of ship, 11 m.	2·20 ,,	—	,,	,,	40	40	0·495	1·24	0·122
at 3.22 p.m. to windward	2.29 ,,	—	,,	,,	50	33·3	0·106	0·32	0·115
of ship.	2.36 ,,	—	,,	,,	60	30·2	0·038	0·125	—
	2.52 ,,	—	,,	,,	25	28·7	1·87	6·5	—
	3·3 ,,	—	,,	,,	10	25·6	10·3	40·0	—
	3.11 ,,	—	,,	,,	r	48·5	48·5	100	—

Date, Remarks, etc.	T G.M.T.	α	Light.	β	d metres	V_a k.m.c.	V k.m.c.	p %	λ
SERIES 32. 4.7.'28.	12.52 p.m.	62	Bright Sun	6	r	126	126	100	—
L Photometer. At El.	1.2 ,,	61	,,	,,	5	123	43·8	35·6	0·156*
Wind S.W., freshening.	1.12 ,,	,,	,,	,,	10	122·5	21·8	17·8	0·148
Moderate swell, surface	1.19 ,,	60	,,	,,	15	122	9·9	8·1	0·143
waves breaking. Bright	1.24 ,,	59	,,	,,	20	122·5	5·2	4·25	—
sun with a few low clouds. High water 6.36 p.m. Secchi disc 11 m. at 12.8 p.m. in shadow of ship, 11·5 m. at 12.14 p.m. in sun (V_a=128,000 m.c.).									
SERIES 33. 11.7.'28.	11.55 a.m.	62	Bright Sun.	3	r	130·5	130·5	100	—
L Photometer. At El.	12.13 p.m.	,,	Light clouds	,,	5	126·5	53	42	0·123*
Very little wind. Light	12.20 ,,	,,	at times	2	10	95·5	23·7	24·8	0·108
variable, owing to passage	12.28 ,,	,,	,,	2·5	15	113	16·0	14·2	0·137
of light clouds across sun.	12.39 ,,	,,	,,	3	20	139·5	8·7	6·25	0·164
High water 11.40 a.m.	12.47 ,,	,,	,,	2·5	25	105·5	2·90	2·75	0·107
	12.54 ,,	61	,,	,,	30	104·5	2·24	2·14	0·081
	12.59 ,,	,,	,,	,,	35	108·5	1·32	1·22	—
SERIES 34. 11.7.'28.	1.19 p.m.	59	Bright Sun.	2·5	r	99	99	100	—
K Photometer. Other	1.29 ,,	58	Light clouds	,,	5	109·5	52·5	48	0·080*
conditions as in Series 33.	1.46 ,,	57	at times	,,	10	114	43·2	37·9	0·092
Water surface glassy at	1.52 ,,	56	,,	3	20	115·5	14·5	12·0	0·125
end of series. Secchi disc	1.59 ,,	,,	,,	,,	25	115	6·85	5·95	0·129
18·5 m. at 3.28 p.m. in	2.6 ,,	55	,,	2·5	30	111	3·66	3·30	0·129
shadow of ship, 16 m. at	2.18 ,,	54	,,	,,	35	107·5	1·76	1·64	0·126
3.33 p.m. in sun (V_a=	2.30 ,,	52	,,	,,	45	109·5	0·55	0·50	0·110
76,000 m.c.).	2.38 ,,	51	,,	,,	55	108	0·194	0·180	0·117
	2.47 ,,	50	,,	,,	65	95	0·046	0·048	—
	2.58 ,,	49	,,	,,	35	94·5	1·09	1·15	—
	3.12 ,,	47	,,	2	25	82	4·1	5·0	—
	3.23 ,,	45	,,	,,	r	87	87	100	—
SERIES 35. 23.7.'28.	11.36 a.m.	58	Bright Sun	4·5	r	118	118	100	—
L Photometer. At El.	11.52 ,,	59	,,	,,	a	121	118·5	98	—
Wind W., light. Sea	12.4 p.m.	,,	,,	,,	5	121	60·5	50	0·092*
calm. Sky clear with	12.8 ,,	,,	,,	,,	10	119	40·2	33·7	0·081
light clouds low on the	12.16 ,,	,,	,,	,,	15	120	26·6	22·2	0·117
horizon. High water	12.20 ,,	,,	,,	,,	20	120·5	12·6	10·45	0·179
9.52 a.m.	12.29 ,,	,,	,,	,,	25	120·5	4·45	3·69	0·228
	12.34 ,,	,,	,,	,,	30	118	1·26	1·07	0·196
	12.37 ,,	,,	,,	,,	35	121·5	0·63	0·52	—
SERIES 36. 23.7.'28.	12.52 p.m.	59	Bright Sun	4	r	119·5	119·5	100	—
K Photometer. Other	12.57 ,,	58	,,	,,	a	120	121	101	—
conditions as in Series 35.	1.9 ,,	,,	,,	,,	5	119·5	68·5	57·5	0·059*
Secchi disc 17·5 m. in	1.24 ,,	57	,,	,,	10	117	55	47	0·086
shadow and lee of ship at	1.30 ,,	,,	,,	,,	20	116·5	18·4	15·8	0·117
3.26 p.m., 14 m. in sun to	1·40 ,,	56	,,	3·5	25	114	9·3	8·15	0·182
windward.	2.0 ,,	54	,,	,,	35	110	1·12	1·02	0·196
	2.17 ,,	52	,,	,,	45	107	0·174	0·162	0·163
	2.24 ,,	51	,,	,,	50	108	0·096	0·089	0·142
	2.28 ,,	50	,,	,,	55	107	0·042	0·039	0·155
	2.34 ,,	49	,,	,,	60	106	0·020	0·019	—
	2.46 ,,	47	,,	,,	35	105·5	1·03	0·98	—
	2.58 ,,	45	,,	3	25	103	4·25	4·1	—
	3.19 ,,	43	,,	,,	r	103·5	103·5	100	—
SERIES 37. 9.8.'28.	11.36 a.m.	55	Weak Sun	1·5	r	56	56	100	—
L Photometer. At El.	11.45 ,,	,,	,,	,,	5	53·5	16·0	29·9	0·196
Sun and light clouds.	11.51 ,,	56	,,	,,	10	52	6·2	11·9	0·168
Dark currents rather	11.55 ,,	,,	,,	,,	15	52·5	2·92	5·55	0·206
troublesome. High water	11.57 ,,	,,	,,	,,	20	55	0·83	1·51	—
10.57 a.m.									

Date, Remarks, etc.	T G.M.T.	α	Light.	β	d metres	V_a k.m.c.	V k.m.c.	p %	λ
SERIES 38. 9.8.'28.	12.51 p.m.	55	Weak Sun	1·5	r	47	47	100	—
K Photometer. Other	12.58 „	„	„	„	5	53	18·1	34·2	0·170*
conditions as in Series 37.	1.4 „	„	„	„	10	43	6·7	15·5	0·194
Secchi disc 10 m. in	1.14 „	54	Cloudy	1	20	28·0	0·525	1·87	0·178
shadow of ship and 9 m.	1.29 „	53	„	„	25	33·2	0·357	1·07	0·065
in sun at 3.30 p.m. (V_a	1.58 „	50	Weak Sun	1·5	30	42	0·41	0·975	0·054
about 50,000 m.c.).	2.10 „	49	„	„	35	41·5	0·259	0·625	0·098
	2.32 „	47	Cloudy	1	40	28·8	0·105	0·365	0·112
	2.36 „	46	„	„	45	27·1	0·054	0·199	0·129
	2.40 „	45	„	„	50	27·6	0·028	0·100	—
	2.54 „	43	Weak Sun	1·5	20	38·5	1·42	3·70	—
	3.12 „	41	„	„	10	39·2	7·65	19·6	—
	3.22 „	40	„	„	r	52·5	52·5	100	—
SERIES 39. 29.8.'28.	12.4 p.m.	49	Bright Sun	4	r	108·5	108·5	100	—
L Photometer. At E1.	12.10 „	„	„	„	5	109·5	52·5	48	0·126*
Wind S.W., light. Con-	12.17 „	„	„	„	10	109·5	26·3	24·0	0·119
siderable swell, some	12.22 „	„	„	„	15	108	15·8	14·6	0·104
waves breaking. Clear	12.26 „	„	„	„	20	109	9·2	8·45	0·164
sky with light clouds.	12.32 „	„	„	„	25	108	3·04	2·82	0·127
High water 4.38 p.m.	12.44 „	„	„	„	30	111·5	2·64	2·36	0·068
	12.50 „	„	„	„	35	109·5	1·56	1·42	—
SERIES 40. 29.8.'28.	1.5 p.m.	48	Bright Sun	4	r	110	110	100	—
K Photometer. Other	1.10 „	47	„	„	5	97	46·5	48	0·100*
conditions as in Series 39.	1.13 „	„	„	„	15	97·5	21·1	21·6	0·090
Secchi disc 15 m. on lee	1.33 „	46	„	„	20	106·5	13·15	12·3	0·134
and shadow side of ship,	1.44 „	„	„	„	30	104·5	3·03	2·90	0·138
but illuminated by sun-	1.56 „	45	„	„	40	101	0·775	0·765	0·103
light passing under the	2.0 „	44	Light Cloud	2	40	55·5	0·435	0·785	„
keel, at 3.28 p.m., 14 m.	2.4 „	43	„	„	50	56	0·204	0·365	0·108
on weather side (V about	2.24 „	41	Bright Sun	4	50	94	0·306	0·326	„
80,000 m.c.).	2.31 „	40	„	„	60	92·5	0·082	0·088	—
	2.53 „	38	„	3·5	30	85·5	2·42	2·83	—
	3.8 „	37	„	„	r	83·5	83·5	100	—
SERIES 41. 18.9.'28.	1.45 p.m.	38	Sun	2·5	r	78·5	78·5	100	—
K Photometer. At E1.	1.51 „	37	„	„	5	77·5	41·5	53·5	0·086*
Calm. Sky clear after	1.55 „	„	„	„	10	77	27·7	36·0	0·076
thick fog in morning,	1.59 „	36	„	„	15	77	19·2	25·0	0·084
light very steady. High	2.25 „	35	„	2	20	72	11·2	15·6	0·092
water 8.6 p.m. Secchi	2.28 „	34	„	„	25	70·5	7·05	10·0	0·092
disc 16·5 m. in shadow of	2.32 „	33	„	„	30	69	4·3	6·25	0·100
ship and 14 m. in sun at	2.35 „	„	Light Cloud	1·5	35	50	1·84	3·68	0·112
4.30 p.m. (V about 25,000	2.42 „	32	Sun	2	40	68	1·38	2·03	0·117
m.c.).	2.46 „	„	„	„	45	69	0·78	1·13	-
	3.0 „	30	Variable	„	25	67	4·8	7·15	—
	3.16 „	29	Light Cloud	1·5	25	35·8	2·79	7·8	—
	3.24 „	28	„	„	45	34·9	0·435	1·24	—
	3.29 „	27	„	„	55	32·5	0·116	0·357	0·096
	3.35 „	26	„	„	60	38·8	0·114	0·294	—
	3.45 „	25	„	„	25	32·8	3·25	9·9	—
	3.54 „	23	„	„	r	29·2	29·2	100	—
SERIES 42. 2.10.'28.	1.10 p.m.	35	Sun	2·5	38	65	0·365	0·56	—
L Photometer. At E1.	1.14 „	„	„	„	35	65·5	0·445	0·68	0·106
Very faint air from N.W.	1.19 „	34	„	„	30	60	0·785	1·31	0·126
Very slight roll. Sun	1·36 „	33	„	2	25	61	1·46	2·39	0·123
shining through high	1.39 „	„	„	„	20	59	2·66	4·5	0·131
hazy clouds. High water	1.46 „	32	„	„	15	59	5·25	8·9	0·128
7.34 p.m. Flat calm with	1.57 „	31	„	„	10	57	9·2	16·1	0·129
glassy water surface	2·3 „	30	„	„	5	55	17·7	32·2	0·166*
later.	2.11 „	29	„	„	r	54	54	100	—
SERIES 43. 12.10.'28.	12.30 p.m.	32	Sun	2	r	62	62	100	—
J Photometer. About	12.48 „	„	„	„	20	62	0·93	1·50	0·202*
3 m. S.W. of Mewstone.	1.3 „	31	Light Cloud	1·5	40	49·5	0·013	0·026	—
Wind N.E. Considerable	1·18 „	30	Variable	„	20	47·5	0·675	1·42	0·202*
swell. White clouds	1.30 „	29	Cloudy	1	r	30·6	30·6	100	—
moving rapidly across the sky. High water 5.5 p.m. Secchi disc 6·5 m. on either side of ship at 1.40 p.m.									

Date, Remarks, etc.	T G.M.T.	α	Light.	β	d metres	V_a k.m.c.	V k.m.c.	p %	λ
SERIES 44. 30.11.'28.	12.37 p.m.	—	Cloudy	1	r	15·35	15·35	100	—
J Photometer. At E1.	12.52 ,,	—	,,	,,	5	8·9	3·04	34·2	0·156
Wind N.W., fresh.	12.56 ,,	—	,,	,,	10	7·8	1·38	17·7	0·125
Waves breaking. Moder-	12.58 ,,	—	,,	,,	15	8·45	0·83	9·8	0·117
ate short swell. Sky com-	1.1 ,,	—	,,	,,	20	7·05	0·387	5·5	0·103
pletely overcast. High	1.4 ,,	—	,,	,,	25	6·5	0·226	3·48	0·100
water 7.51 p.m. Secchi	1·8 ,,	—	,,	,,	30	7·25	0·146	2·01	0·117
disc 11 m. to windward,	1.11 ,,	—	,,	,,	35	7·45	0·080	1·07	—
9 m. to leeward at 3 p.m.	1.22 ,,	—	,,	,,	15	6·4	0·43	6·7	—
	1.40 ,,	—	,,	,,	35	6·3	0·53	0·84	—
	1.50 ,,	—	,,	,,	40	7·6	0·030	0·395	0·141
	1.56 ,,	—	,,	,,	45	6·4	0·013	0·205	0·123
	2.1 ,,	—	,,	,,	50	5·3	0·006	0·115	0·082
	2.14 ,,	—	,,	,,	55	5·75	0·005	0·085	—
	2.34 ,,	—	,,	,,	25	6·65	0·170	2·56	—
	2.48 ,,	—	,,	,,	r	5·1	5·1	100	—
SERIES 45. 2.1.'29.	12.35 p.m.	—	Cloudy	1	5	15·0	6·3	42	0·127*
L Photometer. At E1.	12.45 ,,	—	,,	,,	10	12·45	2·98	23·9	0·101
Strong N.E. wind.	12.52 ,,	—	,,	,,	15	13·7	2·10	15·3	0·097
Waves breaking every-	12.59 ,,	—	,,	,,	20	15·25	1·39	9·1	—
where. Very heavy swell.									
Cloudy sky. Light very									
variable. High water									
11.5 p.m.									
SERIES 46. 2.1.'29.	1.27 p.m.	—	Cloudy	1	r	7·15	7·15	100	—
J Photometer. Other	1.34 ,,	—	,,	,,	5	7·65	2·66	34·8	0·138*
conditions as in Series 45.	1.47 ,,	—	,,	,,	15	9·4	1·01	10·7	0·106
	1.52 ,,	—	,,	,,	25	7·45	0·315	4·25	0·082
	1.54 ,,	—	,,	,,	35	7·5	0·156	2·08	—

Series 28, obtained on April 19th, is remarkable for the high value of V_a, i.e. 134,000 m.c., obtained at 12.56 p.m. with a solar altitude of 51°. This value was the highest but one obtained during the year, and is probably attributable to the combination of clear sun and white clouds close to it. The value found for β at 12.4 p.m. was 3·75. We may compare this with the vertical illumination, 126,000 m.c., found in Series 32 on July 4th at 12.52 p.m. with α=62°. The only clouds in the sky on this occasion were low down, and the diffuse light was remarkably low, the value found for β being over 6, which is quite exceptional. This would give 105,000 m.c. as the pure sunlight in V_a on July 4th, as compared with 98,000 m.c. on April 19th.

The highest value recorded for V_a during the year was 139,500 m.c. at 12.39 p.m. on July 11th, α being 62° (Series 33). On this occasion, also, the diffuse light was increased by the reflection from white clouds, as is shown by the fact that a measurement of β at 12.36 p.m. gave a value as low as 3·14 with V_a=137,000 m.c. This would mean that at 12.39 p.m. the direct sunlight amounted to about 95,000 m.c., and the diffuse light to about 44,500 m.c.

Series 28 is also interesting as showing the small effect of sudden changes of surface light on the percentage illumination at any depth. An examination of the readings from 12.31 to 12.50 p.m. and from 3.53 to 4.1 p.m. shows that the passage of a cloud across the sun reduces

the aerial and submarine illuminations in about the same ratio. This accords with all our previous experience that the vertical absorption coefficient of the sea is but little affected by the obliquity of the incident light. It would seem, as already suggested, that the surface and surface layers generally have sufficient diffusing properties to control the average obliquity of the light in the deeper layers.

TABLE II.

Station E1, Collected Results.

Series.	Date.	p_{20}	p_{40}	p_{60}	λ_{0-20}	λ_{20-40}	λ_{40-60}
6	1.10.'25	5·86	0·25	—	0·134	0·157	—
9 & 10	5.9.'27	0·394	—	—	0·268	—	—
11	7.9.'27	0·398	0·013	0·002	0·268	0·170	0·086
12	„	0·126	—	—	0·325	—	—
18	3.10.'27	4·74	0·665	0·088	0·144	0·098	0·101
23	1.3.'28	8·0	1·20	0·063	0·118	0·095	0·147
26	27.3.'28	4·6	0·248	—	0·145	0·146	—
27	5.4.'28	5·2	0·58	0·057	0·139	0·110	0·116
28	19.4.'28	14·6	2·11	0·244	0·088	0·096	0·108
29	7.5.'28	14·1	1·76	0·240	0·090	0·104	0·100
30 & 31	13.6.'28	8·6	0·73	0·125	0·115	0·123	0·088
32	4.7.'28	3·96	—	—	0·153	—	—
33 & 34	11.7.'28	8·0	0·765	—	0·118	0·117	—
35 & 36	23.7.'28	10·5	0·393	0·019	0·104	0·164	0·151
37 & 38	9.8.'28	2·28	0·356	—	0·181	0·093	—
39 & 40	29.8.'28	9·0	0·78	0·088	0·112	0·122	0·109
41	18.9.'28	14·4	2·02	0·254	0·089	0·098	0·104
42	2.10.'28	4·4	0·382	—	0·148	0·122	—
44	30.11.'28	5·6	0·445	0·046	0·136	0·126	0·114
45 & 46	2.1.'29	7·7	1·22	—	0·120	0·092	—
Mean		6·62	0·72	0·085	0·150	0·120	0·111

Table II shows the percentage illuminations at 20, 40, and 60 metres, respectively, for all the series obtained so far at E1, and also the values of the mean absorption coefficients for the intervals 0 to 20, 20 to 40, and 40 to 60 metres. All series obtained closer in-shore have been omitted from this table, which is an attempt to show the seasonal changes in opacity.

When two series were taken on one day their results have been combined in the table, except in the case of Series 11 and 12. These were obtained in the autumn of 1927, when the water was very opaque, and such a large increase occurred in the opacity of the surface layers between the two series that the results differed entirely, and are shown separately. The percentage recorded at any depth is the mean of all values obtained at that depth or calculated for it from values obtained for levels within 5 m. above or below. In the single case of Series 30 and 31, as no readings were taken in Series 31 between 10 m. and 30 m., the geometric mean of the percentages at these levels was used, and

combined with the 20 m. percentage of Series 30 to obtain the value given.

The values of λ, which measures the opacity of the water, are calculated from the mean percentages. A mean surface loss of 15% is assumed in finding λ_{0-20}.

Hence, since $\frac{\log_e 10}{20} = 0{\cdot}115$, $\lambda_{0-20}=0{\cdot}115$ (log 85—log p_{20}), $\lambda_{20-40}=0{\cdot}115$ (log p_{20}—log p_{40}), and $\lambda_{40-60}=0{\cdot}115$ (log p_{40}—log p_{60}).

In finding the mean values of p given in the last line allowance has been made for the fact that occasionally, when the surface water was rather opaque, so that p_{20} was low, there was not sufficient light to measure at 60 m. and p_{60} is missing. Sometimes even p_{40} is absent. Thus, the simple averages of the figures given would exaggerate the percentages for the lower levels by eliminating the values corresponding to high opacity.

Accordingly, the average values of p_{20} were found, (a) for all the series, (b) for series containing values of p_{40}, and (c) for series containing values of p_{60}. The three means were 6·62, 7·53, and 8·65, respectively. The average of the values of p_{40} was, accordingly, multiplied by 6·62/7·53, and that for p_{60} by 6·62/8·65. This will give a fair representation of the mean percentages if the average opacity of the lower layers is independent of that of the surface layer. This assumption seems to be borne out by the readings, as we sometimes find very clear water underlying very opaque water (Series 11), while occasionally the effect is reversed (Series 35 and 36).

The mean values of the absorption coefficients are the simple averages of the figures in the columns, since, as we have seen above, there is no reason to suppose that a high opacity in the upper layer would correspond to a high opacity lower down. It must be noted that the mean opacities found in this way, though shown in the same line as the mean values of p, differ appreciably from the opacities that would be found by calculation from the mean percentages, since the latter are the arithmetic, and not the geometric means of the individual values.

Visibility of the Secchi Disc.

Table III shows a comparison of the maximum depth of visibility of the Secchi disc with other data from Series 23 to 44. The values of V_a are, in some cases, estimates from photometer readings taken a little time before or after. D is the maximum depth of visibility on whichever side of the ship gave the greatest value. The percentage illumination P at the depth D is found from the value of the product $D\lambda_{0-20}$ assuming a surface loss of 15%.

It will be seen that $D\lambda_{0-20}$ varies less than either D or λ_{0-20}, its mean value being 1·70. Hence, a very rough rule for finding the opacity is $\lambda_{0-20}=1{\cdot}7/D$. Another way of expressing the same statement is that the percentage illumination at the limit of visibility is about 16%.

There seems to be no relation between D and either β or V_a. V, the illumination at the limit of visibility, varies between 800 and 18,700 m.c. This is entirely in accord with some previous observations, which showed that the visibility of the disc was not affected by the approach of night-fall until the light became so poor that the adaptive power of the eye could no longer compensate for the reduction.

TABLE III.

Visibility of the Secchi Disc.

Series.	Date 1928	Time G.M.T. p.m.	β	V_a k.m.c.	D m.	λ_{0-20}	$D\times\lambda_{0-20}$	P	V k.m.c.
23	1, 3	4.30	2	25	14	0·118	1·65	16·2	4·0
24	6, 3	2.40	2·5	60	13·5	0·151	2·04	11·0	6·6
27	5, 4	4.15	2	55	10	0·139	1·39	21·2	11·6
28	19, 4	4.18	3	65	18	0·088	1·58	17·4	11·3
29	7, 5	4.5	1	18·7	22	0·090	1·98	11·7	2·2
30 & 31	13, 6	3.17	1	40	14	0·115	1·61	15·9	6·4
32	4, 7	12.14	6	128	11·5	0·153	1·76	14·6	18·7
33 & 34	11, 7	3.28	2	87	18·5	0·118	2·18	9·6	8·4
35 & 36	23, 7	3·26	3	100	17·5	0·104	1·82	13·7	13·7
37 & 38	9, 8	3·30	1·5	50	10	0·181	1·81	13·9	7·0
39 & 40	29, 8	3·28	3	80	15	0·112	1·68	15·8	12·6
41	18, 9	4.30	1·5	25	16·5	0·089	1·47	19·5	4·9
43	12, 10	1.40	1	30	6·5	0·203	1·32	22·6	6·8
44	30, 11	3.0	1	4·5	11	0·136	1·50	18·8	0·8
					Mean		1·70	15·8	

It would seem, then, that we may use the Secchi disc to estimate the opacity of the water without paying any attention to even comparatively large variations in the brightness of the daylight. On the other hand, the large variations recorded in the penultimate column of Table III show that other sources of error, which must always be large where a visual estimate has to be made under very varying conditions, prevent the method from being anything more than a rough approximation.

In the 1928 paper we mentioned the desirability of trying a water telescope through which to view the Secchi disc. With any form of rigid tube it would be quite impossible to keep the disc in view when the ship was rolling more or less heavily, as was almost always the case. Accordingly attempts were made to use a wide cloth tube, about 0·3 metre in diameter and 2 m. in length. The attempts were, however, quite unsuccessful. Trials were also made with a Nicol prism, which under certain conditions extinguishes reflections from water, but with the

very broken water surfaces usually encountered there was a positive disadvantage in its use. We were no more successful with various colour screens, though certain of these were often of use in picking up objects on the shore in hazy weather. The depths recorded for the visibility limit of the disc are those obtained by the youngest of the deck hands, who has remarkably good sight and could often see the disc half a metre or a metre further down than we could.

Reliability of Data.

Before discussing the interpretation of the results, it is necessary to consider what differences in the value of λ are significant. It was concluded in the previous work (1928) that the two photometers, L (vacuum) and K (gas-filled) gave results which were generally in agreement. In the course of the present work, K and L were compared very thoroughly, and were found to be in close agreement at times, so that one can rely on the differences, when found, as being of definite significance. Table IV contains data from Series 21 (see **3**, p. 474), obtained with photometer K, and shows the consistency of the results obtained under certain conditions. Furthermore, the altitude of the sun appears to have but little influence upon the value of λ though a slight rise occurred as the morning advanced and the altitude increased. On this occasion β was approximately 2, so that about half of the total light was direct sunlight.

TABLE IV.

From Series 21, Photometer K.

Hour.	α	d	λ
11.22	24°	0–10	0·160
9.36	26°	0–20	0·130
10.21	30°	0–20	0·134
11.50	35°	0–20	0·137
9.22	24°	0–40	0·121
10.28	31°	0–40	0·121
12.6	35°	0–40	0·124

Table V records values of λ obtained with the two photometers. The results agree closely at 10, 15, and 20 metres. There is an indication that the more opaque layers are found at lesser depths as the day goes on. The differences in the values of λ are quite unconnected with any slight differences in salinity, nor does there appear to be any relation between the value of λ and the temperature of the water. This point will be mentioned again later.

The values of λ for the layer next the surface is affected by the surface loss which is somewhat variable. The unsteadiness of the light just below the surface renders any method of measurement involving a telephone balance unsuitable for measuring this loss accurately, save under exceptionally favourable conditions. Moreover, a diffusing window is absolutely essential for this purpose, as the obliquity correction for the different conditions above and below the surface with the ground-glass window used in Series 7 to 23, inclusive, was too uncertain to justify any importance being attached to measurements of surface loss.

TABLE V.

Station E1, Series 9, 12.14–1.13 G.M.T. downwards.
„ 10, 2.0 –2.18 „ downwards.
„ 10, 2.32–2.48 „ upwards.
„ 11, 1.22–2.23 „ downwards.
„ 12, 3.12–3.28 „ downwards.

Series 9 and 10, $\beta = 1$. Series 11, $\beta = 4$. Series 12, $\beta = 3$.

	Series 9 and 10 on 5.9.'27.				Series 11 and 12 on 7.9.'27.		
d	λ (K)	λ (L)	λ (L)	t°	S °/₀₀	λ (K)	λ (L)
0	—	—	—	16·1	35·13	—	—
2·5	—	0·349*	0·356*	—	—	0·318*	0·523*
5	0·350*	0·318	0·294	—	—	0·308*	0·387
10	0·268	0·266	0·232	15·82	35·16	0·293	0·306
15	0·215	0·212	0·217	15·76	35·12	0·267	0·208
20	0·151	0·168	0·170	15·10	35·17	0·206	0·175
25	0·106	—	—	13·80	35·19	0·179	-
30	—	—	—	—	—	0·148	-
35	—	—	—	—	—	0·128	—
40	—	—	—	—	—	0·128	—
45	—	—	—	—	—	0·082	—
50	—	—	—	13·36	35·20	0·051	—
55	—	—	—	—	—	0·061	- -
70	—	—	—	13·36	35·20	—	—

The temperature and salinity measurements refer to September 7th, but must be close approximations for September 5th also. The letters in brackets indicate the photometer, K or L, used.

Pending the results of further measurements of surface loss, which we hope to make by means of the time-integrating Neon Lamp Photometer devised by Dr. J. H. J. Poole (**4**), we have, throughout, assumed a surface loss of 15% as the mean of the results obtained with a diffusing window in Series 1 to 6. The largest surface loss recorded in these series was 31% (Series 4) and the smallest 5% (Series 6).

It is evident that this assumption of a uniform loss will give us too small values of λ for the upper layer when the surface is smooth and the

surface loss small, and too high values for rough conditions, when the surface loss is large. The differences, however, are not very important. Remembering that $\lambda=\frac{2\cdot3}{10}(\log p_0-\log p_{10})$, where λ refers to a layer 10 metres thick, p_0 and p_{10} being the percentage illuminations just below the surface and at a depth of 10 metres, respectively, we readily find that the use of 85% instead of 95%, as the value of p_0 on a very calm day, would reduce λ by 0·011. Similarly if the surface loss were as high as 31% λ, as calculated, would be 0·021 too high.

These errors would not be of very great importance compared with the variations observed for λ. Moreover, for the values of λ given in Table II for layers 20 m. thick the errors for the upper layer would be only 0·005 and 0·010, respectively.

It is probable that errors due to the shadow of the ship are at least as important as those due to variations in the surface conditions.

Again, in deep water, the readings, though usually very steady, are small, and, consequently, even minute dark currents become highly important. Their presence, however, was carefully checked by closing the photometer window at each depth. The earlier series were also subject to a small error from soakage effects. These were eliminated by leaving the high tension plugged in continuously, and in the new arrangement, shown in the figure, this permanent connection of the high tension has been protected from any accidental displacement.

Bearing in mind these possible sources of error, one may arrive at an idea of the reliability of the various measurements, yet it is scarcely possible to assign a definite percentage value to the error, as the external conditions vary so much when the sea is rough. In particular, an error may arise through a small wave increasing the height of the column of water above the photometer, though unable to raise the ship bodily or, alternatively, the motion of the ship may raise or lower the photometer, thus rendering the light unsteady and hard to measure accurately. With the photometer at 10 metres, namely, in determining the value of λ for 5 metres, it is unlikely that the depth error ever exceeds 1 metre; 0·5 metre seems, however, quite a possible value. Again, the shading due to the ship becomes relatively more important on a dull day than on a sunny day, when the greater proportion of the illumination is due to direct sunlight if due care is taken to keep the photometer out of the direct shadow.

The error due to the cable suspending the photometer not being perpendicular when the ship is drifting, has already been shown to be negligible (1926, p. 189).

To sum up, it is probably safe to conclude that with photometers K and J between 10 and 30 metres or with photometer L between 10 and

25 metres, a 10% error in λ is unlikely, a 5% error is unusual, and the results are often considerably more accurate.

Causes of the Observed Significant Differences in the Values of the Absorption Coefficient.

In our 1928 paper, we suggested that the variation in the values of λ was due to the different horizontal distribution of the phytoplankton and to the zooplankton ascending or descending according to the position of the optimum light intensity for each species. We attributed the much greater clearness of the water in winter as compared with September to the fact that the sea is far poorer in plankton in mid-winter than in autumn. The high opacity of the surface layers which occurred in the autumn of 1927, and declined with the approach of winter, was not repeated in 1928, nor was it found off-shore in 1925, so the conditions in 1927 appear to have been somewhat abnormal. There is, of course, a certain absorption of light, due to inorganic matter in suspension, at all times of the year, for the whole of the English Channel is subject to detrital sedimentation. The present paper contains the results of an examination of the water throughout an entire year. We have, in addition, the data from September to December, 1927. It may be said at once that no single factor appears to be responsible for the variation in the values of λ throughout the year and throughout the day. As possible causes, we have to consider the inorganic material in suspension, the phytoplankton, the zooplankton, and the organic *débris* resulting from the living organisms or derived from the land or the bottom. Since the phytoplankton are developed near the surface in those layers in which the illumination is adequate, and since in summer the upper 15 to 25 metres is also warmer, one might expect to find some correlation between the temperature of the water and the value of λ. Table VI shows the temperatures and the values of λ obtained with the different photometers at Station E1. It should be added that Series 22 of December 14th, 1927, relates to a position near the Eddystone Lighthouse, which is 10 miles nearer shore than is Station E1. It has been inserted on account of its being the only measurement available for that winter, and the water further out to sea must have been at least as clear as at the Eddystone. Inspection of the data in Table VI reveals no such supposed correlation between high values of λ and the warm surface layer, save in September, 1927. In July, 1928, however, the clearest water was found near the surface, consequently, the view that the phytoplankton is a really important factor in causing the absorption of light in the sea must be ruled out, though it would be premature to conclude that it is of no importance.

TABLE VI.

Ser.	6		9	10		11	12	18		22		23		26	
	1/10/'25		5/9/'27		7/9/'27			3/10/'27		14/12/'27		1/3/'28		27/3/'28	
m.	t° C.	λ (K)	λ (K)	λ (L)	t° C.	λ (K)	λ (L)	t° C.	λ (K)	t° C.	λ (K)	t° C.	λ (K)	t° C.	λ (K)
0	14·9	—	—	—	16·1	—	—	13·9	—	11·8	—	9·7	—	9·6	
2·5	—	—	—	0·349*	—	0·318*	0·523*	—	—	—	—	—	—		
5	14·50	0·134	0·350*	0·318*	—	0·308*	0·387	13·80	0·166*	11·8	0·128	9·45	0·127*	9·62	0·172*
10	14·00	—	0·268	0·266	15·82	0·293	0·306	—	0·099	—	0·110	9·32	0·103	—	0·126
15	13·83	0·143	0·215	0·212	15·76	0·267	0·208	13·80	0·115	—	—	—	0·099	—	0·117
20	13·70	—	0·151	0·168	15·10	0·206	0·175	—	0·149	11·8	0·098	—	0·103	9·60	0·145
25	—	0·162	0·106	—	13·83	0·179	—	13·76	0·121	—	—	9·32	0·101	—	0·162
30	13·60	—	—	—	—	0·148	—	—	0·063	—	0·077	—	0·094	—	0·160
35	—	—	—	—	—	0·128	—	—	0·080	—	—	—	0·101	—	0·127
40	13·58	—	—	—	—	0·128	—	—	0·089	—	—	—	0·109	—	—
45	—	—	—	—	—	0·082	—	—	0·127	11·8	—	—	0·127	—	—
50	13·59	—	—	—	13·36	0·051	—	13·71	0·108	—	—	—	0·138	—	—
55	—	—	—	—	—	0·061	—	—	0·068	—	—	—	0·156	—	—
60	—	—	—	—	—	—	—	—	0·129	—	—	—	0·198	—	—
65	—	—	—	—	—	—	—	—		—	—	—	0·144	—	—
70	13·57	—	—	—	13·36	—	—	13·70		—	—	9·19	—	9·60	—

TABLE VI—(*continued*).

Ser.	27		28		29		30		31	32		33		34		35	36
	5/4/'28		19/4/'28		7/5/'28		13/6/'28			4/7/'28		11/7/'28				23/7/'28	
m.	t° C.	λ (K)	t° C.	λ (K)	t° C.	λ (K)	t° C.	λ (L)	λ (K)	t° C.	λ (L)	t° C.	λ (L)	λ (K)	t° C.	λ (L)	λ (K)
0	—	—	10·1	—	12·5	—	13·1	—	—	14·1		16·1	—	—	18·3	—	—
2·5	—	—	—	—	—	—	—	—	—	—	—	—	—	—		—	—
5	9·80	0·139*	10·10	0·090*	12·20	0·097*	13·10	0·133*	0·105*	13·85	0·156*	14·79	0·123*	0·080*	18·06	0·092*	0·059*
10	—	0·128	—	0·077	10·96	0·070	12·71	0·106	—	13·61	0·148	14·11	0·108	0·092	17·41	0·081	0·086
15	—	0·129	10·04	0·078	10·32	0·083	—	0·116	—	13·43	0·143	13·71	0·137	—	15·13	0·117	—
20	—	0·144	—	0·079	10·30	0·099	12·42	0·114	—	13·41	—	13·21	0·164	0·125	12·76	0·179	0·117
25	9·70	0·132	—	0·075	—	0·101	—	0·141	—	13·25	—	12·35	0·107	0·129	12·62	0·228	0·182
30	—	0·092	9·98	0·088	10·25	0·099	12·35	0·141	0·106	11·82	—	11·85	0·081	0·129	12·60	0·196	—
35	—	0·103	—	0·119	—	0·104	12·26	0·166	—	—	—	—	—	0·126	—	—	0·196
40	—	0·115	—	0·121	—	0·122	11·83	—	0·122	11·72	—	11·82	—	—	12·54	—	—
45	—	0·108	—	0·114	—	0·100	—	—	—	—	—	—	—	0·110	—	—	0·163
50	—	0·135	—	0·115	—	0·091	11·24	—	0·115	11·72	—	—	—	—	12·46†	—	0·142
55	—	0·129	—	0·109	—	0·111	—	—	—	—	—	—	—	0·117	—	—	0·155
60	—	—	—	0·100	—	0·085	—	—	—	—	—	—	—	—	—	—	—
65	—	—	—	0·090	—	0·060	—	—	—	—	—	—	—	—	—	—	—
70	—	—	9·95	—	10·25	—	11·24	—	—	11·72	—	11·78	—	—	12·92†	—	—

† A second bottle gave 12·65 for 50 m. and 12·87 for 70 m.; 90 min. later 70 m. gave 12·76.

Ser.		37	38		39	40		41		42		44		45	46
		9/8/'28			29/8/'28		18/9/'28		2/10/'28		30/11/'28		2/1/'29		
m.	t° C.	λ (L)	λ (K)	t° C.	λ (L)	λ (K)	t° C.	λ (K)	t° C.	λ (L)	t° C.	λ (J)	t° C.	λ (L)	λ (J)
0	16·7	—	—	15·9	—	—	16·8	—	14·95	—	12·2	—	10·5	—	—
2·5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5	16·54	0·196*	0·170*	15·68	0·126*	0·100*	16·62	0·086*	14·73	0·166*	12·17	0·156*	10·70	0·127*	0·138*
10	16·45	0·168	0·194	15·68	0·119	—	16·46	0·076	14·73	0·129	—	0·125	—	0·101	—
15	16·31	0·206	—	15·09	0·104	0·090	16·32	0·084	14·71	0·128	—	0·117	10·72	0·097	0·106
20	15·91	—	0·178	13·61	0·164	0·134	15·55	0·092	—	0·131	—	0·103	—	—	—
25	13·41	—	0·065	13·58	0·127	—	13·76	0·092	14·72	0·123	12·17	0·100	—	—	0·082
30	12·96	—	0·054	13·41	0·068	0·138	13·68	0·100	—	0·126	—	0·117	—	—	—
35	—	—	0·098	—	—	—	—	0·112	—	0·106	—	—	—	—	—
40	12·92	—	0·112	12·92	—	0·103	13·55	0·117	—	—	—	0·141	10·72	—	—
45	—	—	0·129	—	—	—	—	—	—	—	—	0·123	—	—	—
50	12·92	—	—	12·78	—	0·108	—	—	14·72	—	12·17	0·082	—	—	—
55	—	—	—	—	—	—	—	0·096	—	—	—	—	—	—	—
60	—	—	—	—	—	—	13·51	—	—	—	—	—	—	—	—
65	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
70	12·92	—	—	12·76	—	—	13·53	—	14·71	—	12·17	—	10·72	—	—

Previous work on the phosphate content of sea-water has shown that at some time during each spring there is a very rapid diminution, indicating that the multiplication of the diatoms has used up the phosphate. Accordingly, one might expect that the upper layers of the sea would offer greater obstruction to the passage of light immediately after this outburst of diatoms than they did before it. Table VII shows that in 1928 the outburst occurred between April 19th and May 2nd, but the values of λ in Table VI prove that the very clear water present on April 19th persisted through early May. Again, on July 11th and 23rd, the first 15 metres was clear water, whereas on August 9th the clear water was deeper. The phosphate content was, however, closely the same on these three dates.

TABLE VII.

PHOSPHATE IN SEA-WATER, AS mg. P_2O_5 PER m^3, AT STATION E1, 1928.

m.	Mar. 27	April 5	April 19	May 2	May 7	July 11	July 23	Aug. 9
0	28	24	24	10	9	8·5	0	0·5
5	25	25	23	10	9	1·5	0	0
10	—	—	—	—	10	2	1·5	0
15	25	—	—	10	22	2	1·5	0·5
20	—	—	—	17	18	4	10·5	1
25	26	—	—	18	18	8·5	15	10
30	—	—	—	—	19	20	13	13
40	—	—	—	—	—	19	13	—
50	—	26	—	—	—	—	14	12
70	—	27	23	20	19	24	14	19

In the course of the study of the seasonal changes in phosphate at Station E1, extending from 1923 onwards, the conclusion has been reached that the water in this region is but little subject to influx of water from other sources, or, to be more precise, that the water which reached this position had been subjected to similar changes in its phosphate condition. The possibility, however, that some of the changes in the values of λ may be occasioned by the influx of water of different origin must be considered. Table VIII records the salinity at Stations E1, E2, mid-Channel, and E3, off Ushant, from June, 1927, to January, 1929. As a rule the water is of greater salinity at E3 than it is at E2, and the salt content of E2 is usually greater than that of E1. The analyses given were carried out at the Government Chemist's Laboratory, London. It may be concluded that from June up to November, 1927, there was no appreciable movement of water. On December 9th, however, the rather higher salinity indicates movement of water from near E2 towards E1, and this coincides with a clearing of the water. In February, 1928, an abnormal condition obtained, inasmuch as the salinity of the water decreased from E1 to E3. Such a condition was only observed once

TABLE VIII.

SALINITY AT STATIONS E1, 10 MILES S.W. OF THE EDDYSTONE, E2, MID-CHANNEL, AND E3, OFF USHANT, IN PARTS PER 1000; AVERAGED FOR THE WATER COLUMN TO INDICATE MOVEMENT OF WATER TOWARDS E1.

	1927					1927	1928				1928
	June 27	Aug. 2	Sept. 7	Oct. 3	Nov. 4	Dec. 9	Jan. 31	Feb. 21	Mar. 27	Apl. 19	May 2
E1	35·21	35·22	35·17	35·16	35·14	35·23	35·17	35·18	35·12	34·98	34·98
E2	—	35·23	—	—	35·30	—	—	35·09	—	—	—
E3	—	35·30	—	—	—	—	—	35·05	—	—	—

	1928								1929		
	May 8	June 4	July 4	July 23	Aug. 16	Aug. 29	Sept. 18	Oct. 2	Nov. 30	Jan. 2	Jan. 7
E1	34·95	34·90	34·93	34·92	34·90	34·91	35·07	35·02	35·32	35·35	35·39
E2	34·90	—	—	—	35·29	—	—	—	—	—	35·36
E3	34·80	—	—	—	35·36	—	—	—	—	—	—

TABLE IX.

RAINFALL FOR FIVE STATIONS IN BASIN OF R. SEINE AND FOR SIX IN BASIN OF R. LOIRE, GIVEN AS mm. PER MONTH.

	Normal.			1923			1928		
	Jan.	Feb.	Mar.	Jan.	Feb.	Mar.	Jan.	Feb.	Mar.
SEINE									
Chaumont	66	55	65	45	92	64	66	96	68
Chaumont-en-Verin	50	38	44	53	88	69	69	63	55
Paris (Parc St. Maur)	39	31	41	40	64	55	61	56	49
Chartres	40	32	42	34	51	57	95	59	79
Rouen	53	41	48	71	86	65	83	94	39
Total	250	197	240	243	381	310	374	368	290
Gross total	—	—	687	—	—	934	—	—	1032
LOIRE									
Tours	56	48	59	62	111	89	77	85	67
Orleans (École)	43	33	45	61	69	79	45	55	54
Chateauroux	51	41	46	62	69	66	68	62	94
Poitiers	51	39	48	45	74	88	87	90	103
Le Mans (École)	54	39	45	46	92	125	89	61	62
Nantes	71	52	55	38	106	109	96	54	106
Total	326	252	298	314	521	556	462	407	486
Gross total	—	—	876	—	—	1391	—	—	1355
Percentages of normal.									
Seine Total	—	—	—	98	193	129	150	187	121
Gross total	—	—	—	—	—	136	—	—	150
Loire Total	—	—	—	96	207	187	142	162	163
Gross total	—	—	—	—	—	159	—	—	155

before since 1921, namely, in 1923, and the rainfall for that area of France drained by the rivers Seine and Loire was abnormally high during the first three months of that year, and for 1928, as shown in Table IX. Accordingly, we may suppose that the water of the rivers opening on to the Atlantic coast of France was responsible for the abnormal salinity conditions found. The high salinity water persisted around E1, up to March 27th, but on April 19th and early in May less saline water was found at E1. To this influx of mid-Channel water, deduced from the data of Table VIII and the known water movements of the Channel, we must attribute the exceptionally great clearness found from April 19th onwards.

It might be thought that the change in the phosphate content, attributed previously to the diatom outburst, was in reality due to this influx of water from near mid-Channel. There are good reasons, however, for rejecting this view. Firstly, the fact that the change in salinity had already taken place by April 19th, whereas the drop in phosphate content did not take place until after that, and, secondly, that, as shown in Table X, the phosphate content from February to May was very similar at all three stations.

TABLE X.

PHOSPHATE IN SEA-WATER, AS mg. P_2O_5 PER m.^{3}, AT STATIONS E1, E2, AND E3, YEAR 1928.

Large asterisk indicates that bottom has been reached before the depth indicated.

Date	February 21	21	22	May 7	8	9
m.	E1	E2	E3	E1	E2	E3
0	27	11	23	9	7	10
5	27	24	—	9	7	—
10	—	—	—	10	8	13
15	—	—	—	22	17	18
20	—	—	—	18	20	25
25	—	—	—	18	—	26
30	—	—	—	19	19	—
70	28	—	—	19	—	—
80	*	25	—	*	21	—
105		*	25		*	28

This definite connection between the sudden clearing of the water in the spring of 1928 and the variation in salinity will not, however, explain all the variations of λ. It does, however, appear to be the cause of the unusual clearness of the water found at E1 on September 18th,

as shown by the sudden rise in salinity, denoting inflow from near mid-Channel. We are, therefore, faced with the necessity of accounting for the existence of layers of relatively great opacity at different levels, even on the same day and within short periods of time, during which there are no indications of any water movements. For these we may tentatively suggest the vertical movements of the zooplankton as a cause. It is true that zooplankton are fewer in numbers and individually larger than the phytoplankton; they are, however, far more capable of aggregation. Russell (**5**, **6**) has shown in a series of papers that the various members of the zooplankton are distributed at depths depending upon the intensity of the illumination at the time, and upon the duration of that illumination. At dusk the animals tend to be found near the surface. During the night they become more uniformly distributed, and at dawn they are again attracted towards the surface. With the increasing light intensity they move downwards, so that the depth at which they are found depends, not only upon the species and the degree to which they are positively or negatively phototropic, but also upon the time at their disposal for travelling under the influence of the stimulus. It becomes of interest, therefore, to see whether any relation exists between the actual intensity of the light, and the depth at which the maximum value of λ occurs in each series. Table XI contains the relevant data. Values for β have also been included as indicating whether the day as a whole was dull or of moderate or intense sunshine. It may be seen that the values of the vertical illumination V vary fairly widely, but are, as a rule, to be reckoned in thousands of metre candles, and it is remarkable that, whereas in the winter, autumn, and early spring the maximum value of λ is usually found at about 5 metres, yet in late spring and summer it may be found at from 15 to 40 metres. In this connection the results obtained in July and August, 1928, are especially significant. The maximum value of λ was found at 10 and 15 metres on August 9th, a dull day, whereas on July 11th it was found between 20 and 30 metres, on July 23rd, between 25 and 35 metres, and on August 29th, from 20 to 30 metres. These were bright sunny days. There appears, therefore, to be some evidence for considering that the layers in which light absorption is a maximum are those in which the photic stimulus has resulted in an aggregation of the zooplankton. This possibly can, of course, be tested by direct experiment, and it is hoped to do this.

In conclusion, we desire to express our thanks to Captain V. Lord and the crew of the *Salpa* for their great assistance in the transport and handling of the instruments, often under conditions of considerable difficulty, the lowering of the photometers in rough water being no easy matter. Though in use since 1924, none of the apparatus has ever been

TABLE XI.

The values of λ shown are maxima or specially high values for the various series and occurred at the depth, in metres, shown. V denotes the vertical illumination, in thousands of metre candles, at depth tabulated.

Date.	5/9/'27	5/9	5/9	7/9	7/9	7/9	7/9	3/10	14/12	1/3/'28	1/3	27/3	5/4
Ser.	9	10	10	11	11	12	12	18	22	23	23	26	27
d	5	1·2	5	1·2	5	1·2	5	5	5	5	60	5	5
λ	0·350	0·349	0·318	0·318	0·308	0·523	0·387	0·166	0·128	0·127	0·198	0·172	0·139
V	5·69	15·4	4·24	54·5	17·3	22·0	4·10	18·2	6·4	26·1	0·036	18·0	21·4
β	1	1	1	4	4	3	3	3·5	1	4	3	1	1·5

Date.	19/4	19/4	7/5	13/6	13/6	13/6	11/7	11/7	11/7	23/7	23/7	23/7
Ser.	28	28	29	30	30	31	33	34	34	35	36	36
d	40	35	40	5	25	40	20	25	30	25	25	35
λ	0·121	0·119	0·122	0·133	0·114	0·122	0·164	0·129	0·129	0·228	0·182	0·196
V	2·12	4·15	1·53	20·4	1·84	0·495	8·7	6·85	3·66	4·45	9·3	1·12
β	4	4	2	1	1	1	3	3	2·5	4·5	3·5	3·5

Date.	9/8	9/8	29/8	29/8	29/8	18/9	18/9	2/10	2/10	30/11	2/1/'29	2/1/'29
Ser.	37	38	39	40	40	41	41	42	42	44	45	46
d	15	10	20	20	30	35	40	5	20	5	5	5
λ	0·206	0·194	0·164	0·134	0·138	0·112	0·117	0·166	0·131	0·156	0·127	0·138
V	2·92	6·7	9·2	13·1	3·03	1·84	1·38	17·7	2·66	3·04	6·3	2·66
β	1·5	1·5	4	4	4	2	2	2	2	1	1	1

broken or damaged at sea. We desire also to record our indebtedness to the Royal Dublin Society for facilities connected with the construction and standardising of the photometers and to the Marine Biological Association for the major part of the apparatus and for laboratory and sea-going facilities. Our thanks are also due to the Director and Staff of the Research Laboratories of the General Electric Company for their valuable advice, and to Mr. S. G. Monk for assisting in testing for troubles associated with damp weather.

SUMMARY.

Measurements were made, throughout the year 1928, of the penetration of daylight into sea-water in the English Channel. One vacuum and two gas-filled potassium photo-electric cells were used below water. In all save the first series an efficient diffusing surface was used with the photometers so that the corrections for obliquity of illumination, necessary in our earlier work, were rendered almost negligible. From October onwards a more sensitive gas-filled cell was available for use, together with a more powerful amplifier and a more efficient insulation of the high-tension batteries; improvements in the switching of the photometers on and off were also incorporated.

The following conclusions have been reached :—

1. The conclusions put forward tentatively in 1928, concerning the agreement between the vacuum and gas-filled cells, have been substantiated in the main, although the vacuum photometer, which is relatively more sensitive to the blue end of the spectrum, generally indicated rather higher opacities.

2. There are no regular seasonal changes in the opacity of the water. A very high opacity occurred in the autumn of 1927, but this was not repeated in 1928.

3. On one occasion, in April 1928, an unusual degree of clearness of the water has been shown to have been associated with the influx of water of lesser salinity, from further out in the Channel. The clearness of the water at E1 in December, 1927, and September, 1928, is probably due to an influx of clearer water, though the salinity changes indicating this are not so well marked.

4. The main spring diatom outburst in 1928 took place when the water at E1 was exceptionally clear and failed to produce any very noticeable obscuring effect.

5. Changes in the level at which the maximum values of λ occur may be observed in the course of a day and are well marked within the

fortnightly periods of observation. Further evidence has been accumulated in favour of the view, put forward tentatively in 1928, that these changes are due to alterations in the level at which the zooplankton has become aggregated during the execution of phototropic movements. Direct evidence is lacking on this point, but it is hoped that it may be obtained this year.

6. For Station E1 the mean values of the percentages of the light in air reaching 20, 40, and 60 metres were 6·62, 0·72, and 0·085 respectively ; for depths of 0–20, 20–40, 40–60 metres the mean values of λ were 0·150, 0·120, and 0·111. The most turbid water was found at 25 m. on July 23rd, λ being 0·228, with very clear water above, λ 0·081 at 10 m. The clearest water column was on April 19th, λ 0·077–0·121, though on August 9th at 25 and 30 m. values of λ 0·065 and 0·054 respectively were obtained.

7. Measurements down to 25 m. showed that the horizontal light (viz. that falling on a vertical surface) was from 0·61 to 0·47, mean 0·54 of the vertical light. The value is higher than that formerly obtained without an efficient diffusing surface on the photometer.

8. The illumination at the depth (D) at which the Secchi disc is just visible is around 16% of that in air. Very roughly the opacity may be found thus, $\lambda_{0-20} - 1{\cdot}7/D$. The visibility of the disc is independent of the illumination in air, within wide limits.

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Sacconereis of Procerastea.

By

Yô K. Okada,

Naba, Hyogo-ken (Japan).

With 1 Figure in the Text.

A Sacconereis " captured by the tow-net in the Firth of Clyde," according to W. C. McIntosh (1908, p. 223, Fig. 5 f.), differs from any described female bud of Autolytus, or of its allied genera such as Myrianida or Proceræa of Ehlers, especially in respect to the shape and number of ovigerous sacs, which the animal carries on its ventral side. " It appears to be fully a quarter of an inch in length, and is readily discriminated by the absence of the single ventral egg-capsule, the ova being borne in eight conspicuous globular or pear-shaped sacs."

There is no second record of the particular Sacconereis since then, and the parent stock to which the bud belongs remains, of course, unknown. Very fortunately a similar or perhaps the same type of Sacconereis was captured here in the Plymouth district, two miles east of the Eddystone, by the bottom plankton net, October 4th, 1927, and I am greatly indebted to Mr. F. S. Russell of this Laboratory for bringing it to my notice.

As will be seen in the accompanying figure, the specimen resembles very closely the female bud of Procerastea (compare with Allen's Pl. 12, Fig. 5, 1921), instead of Autolytus. The large red eyes with distinct lenses, the anterior pair being very large and ventral in aspect, are nothing more than a common character of the sexual individuals of the Autolytinæ to which the present stolon must also belong, but the appendages connected with the head are rather short and appear thicker than those of Autolytus or Myrianida. The arrangement of these tentacles and tentacular cirri exactly corresponds to that of Procerastea. The head itself seems to be composed of three segments, but separation into prostomium, buccal segment and first setigerous segment is obscure. The three prostomial appendages are all represented as smooth, tapering tentacles. Behind the dorsal eyes there is on each side a pair of rather slender tentacular cirri, and these are followed by a single dorsal tentacular cirrus, which is well in front of the first setigerous segment. The tentacular cirri are directed forwards over the head, and are smooth and tapering

like the tentacles. There are, thus, roughly speaking, nine appendages on the head. The three prostomial appendages are comparatively thick, the median one being nearly as long as the two laterals. The dorsal tentacular cirrus of the buccal segment is slightly longer than the ventral and is almost as long as the similar appendage of the first setigerous segment.

McIntosh has figured a long tentacular cirrus on each side of the succeeding setigerous segments, but in my specimen the 2nd, 3rd, 4th, and 5th segments have no such elongated cirri. The dorsal cirrus in these segments is " a large rounded lobe or swelling of somewhat transparent tissue which occupies the posterior dorso-lateral angle of the segment " (Allen, *l.c.*, p. 135), exactly as in the female bud of *Procerastea Halleziana* (see again Allen's Pl. 12, Fig. 5, 1921). In the 6th setigerous segment the dorsal cirrus is somewhat elongate and tapering toward the tip, but there is still no sign of metamorphosis in the parapodium. With the 7th setigerous segment the special modifications for swimming commence, and the number of modified segments is exactly 14, as in McIntosh's specimen, as well as in the female stolon of *P. Halleziana* in Allen's Pl. 12, Fig. 5. Behind the 20th or last modified segment the notopodia and the swimming setæ are absent, as in the part in front of the 7th setigerous segment, but the dorsal cirri still persist, at first as short tapering processes similar to those in the 6th segment. McIntosh has drawn a pair of long tentacular cirri in each of the segments back to the end of the body. The short tapering cirri in my specimen, however, gradually reduce in length as we proceed backwards, and soon become replaced by small knobs of transparent-looking tissue, like those seen in the anterior unmodified segments. In the Sacconereis in question there are 32 setigerous segments in this posterior region, while the tapering cirri are observed only in the first 4 or 5 segments. The last setigerous segment is followed by the pygidium with the anal cirri as usual.

Eight ovigerous sacs, nearly of the same size, 0·7 mm. long and 0·5 mm. wide, are all of a similar pear shape. They are fixed on the ventral surface of the modified mid-segments in such a way that 4 occur on each side, arranged alternately.

Finally, as to the genetic relationship of the stolon in question, we are almost certainly dealing with the sexual individual of Procerastea, and not with such an individual of Autolytus, Proceræa, Myrianida, or Virchowia. Moreover, the parent stock of *Procerastea Halleziana* does not seem to be rare in this part of south England (Allen, 1921). The Syllid is also described from Boulogne (Malaquin, 1892; Caullery, 1925) and Helgoland (Langhammer, 1928), and in these districts it is found closely associated with colonies of Tubularia. At Plymouth the animal lives upon Syncoryne as well as on Tubularia.

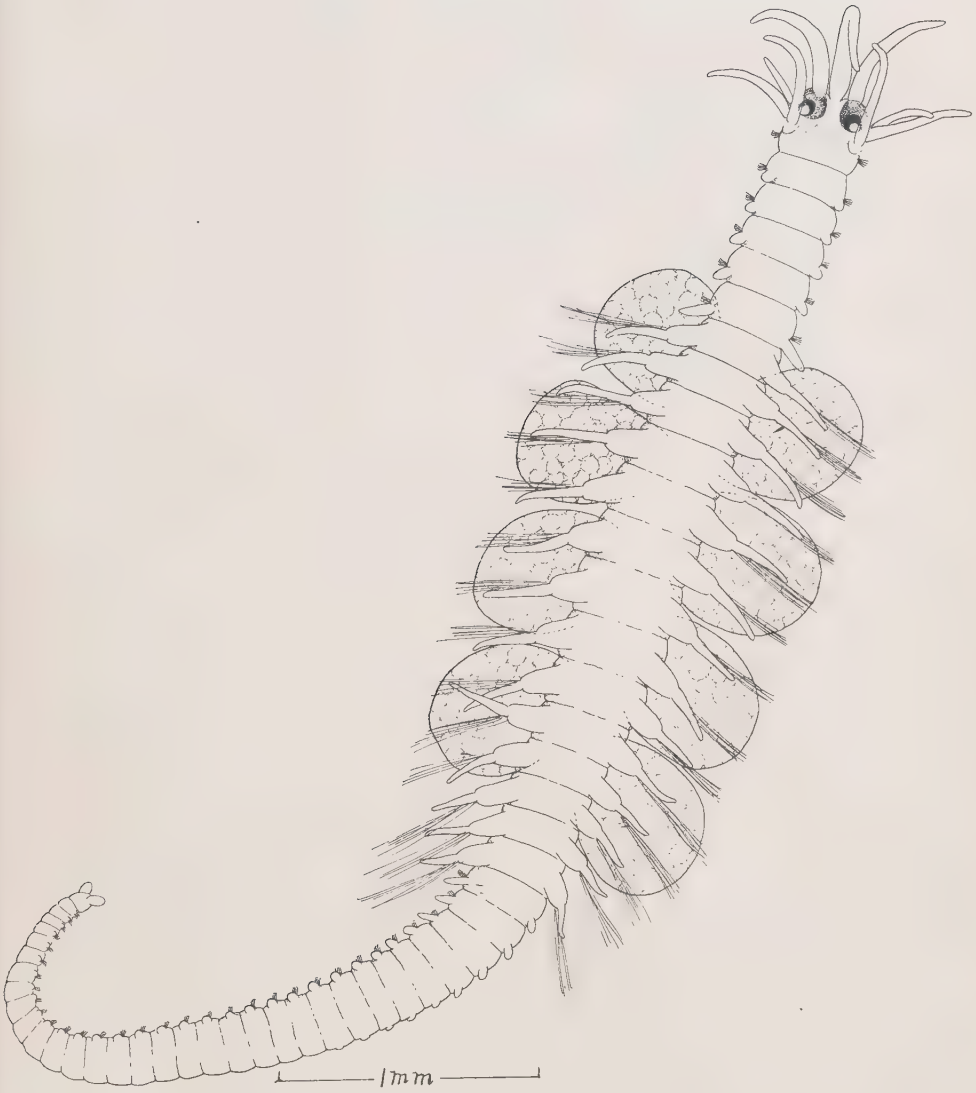

FIG. 1.—Sacconereis, probably of *Procerastea Halleziana*, captured two miles east of the Eddystone. October 4th, 1927.

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Abstracts of Memoirs

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY.

Lecture Experiments on the Hydrogen Ion Concentration Changes in the Rusting of Iron.

By W. R. G. Atkins.

Nature, 1928, **121**, *p.* 615.

The rusting of iron is ordinarily regarded as a slow process, but by adding brom thymol blue to distilled water brought to pH 6·8 by the addition of a trace of bicarbonate, the action of the iron in removing acid from the solution can be observed within two minutes. The ferrous salt thus produced is oxidised at once to ferric, with regeneration of acid. It is possible to follow each step by the use of appropriate indicators. The attack on the iron proceeds, though more slowly, in alkaline solutions in equilibrium with carbon dioxide at a very low pressure.

W. R. G. A.

The Biological Significance of the Unsaponifiable Matter of Oils. III. Fish-Liver Oils.

By H. J. Channon.

Biochem. J., 1928, **22**, *pp.* 51–59.

1. A study has been made of the yields of unsaponifiable matter from the livers of a number of fish.

2. The liver oils of the Selachii differ from those of the Teleostei in that, in many cases, very large amounts of unsaponifiable matter occur in the former.

3. A relationship seems to exist between the percentage of unsaponifiable matter in the liver oils of the Selachii and their sterol content. The higher the percentage of unsaponifiable matter in a given oil the lower is the percentage of sterol in that fraction.

4. Squalene was not detected in the liver oils of any of the fish studied, save in those from three members of the Squalidæ family.

5. The question as to whether squalene is synthesised or is derived by the fish from its food is briefly discussed.

H. J. C.

Further Observations on Phosphagen.

By Philip Eggleton and Grace Palmer Eggleton.

J. Physiol., 1928, **65**, *pp.* 15–24.

Muscles which are capable of rapid energy output are, when resting, richer in phosphagen than muscles of slow-moving type. The muscles of such invertebrates as have been examined contain no phosphagen, or free creatine. *Amphioxus* in this respect resembles the vertebrates. The disappearance of phosphagen in a muscle resting under anaerobic conditions is not directly correlated with the lactic acid production, for the former is practically complete when the latter has only reached a quarter of the value finally attained. The disappearance of phosphagen, whether as the result of fatigue, rigor, or incubation of the minced muscle in bicarbonate buffer in the presence or absence of fluoride, results in the liberation of free creatine. In the presence of fluoride the phosphagen phosphorus becomes acid-stable, presumably being used to form hexose-esters. The reappearance of phosphagen which occurs when a fatigued muscle is allowed to recover in oxygen is very rapid in comparison with the oxidative removal of lactic acid which also occurs. The phosphagen destroyed in a muscle when resting in the absence of oxygen, or when minced and incubated in a bicarbonate buffer solution, is completely accounted for by the orthophosphoric acid produced: phosphagen destroyed during activity appears only in part as free orthophosphate, the remainder (0·40%) appearing as "lactacidogen" phosphorus—i.e. acid-stable organic phosphates rapidly hydrolysed by the muscle enzymes when the chopped muscle is incubated in a bicarbonate buffer.

Über den Auslosungsreiz des Umdrehreflexes bei Seesternen und Schlangensternen.
On the stimulus causing the righting reflex of the starfishes and ophiurians.

By Gottfried Fraenkel.

Zs. f. vergleich. Physiol., 1928, **7**, *pp.* 365–378.

The first phase of the righting movements of the starfishes consists of a dorsal bending of the arms. The latent time of this dorsal bending is exactly the same, if the dorsal sheet and the intestine of the animals are removed, also, if the animals are freely suspended in the water, in any orientation to gravity. Therefore we cannot believe the receptors for the righting reflex to be in sensitive cells of the dorsal sheet (as stated by Mangold, 1921), neither has the intestine the function of a statical organ (as Wolf [1927] has presumed). The dorsal bending of the arms

takes place in all the cases in which the tube feet are not sticking on the bottom. Consequently the stimulus causing the righting movements is due to the not-touching of the tube feet on the bottom. The receptors of the stimulus are the tube feet. There is no more righting reflex, if all the tube feet are cut off.

G. F.

Brown Coloration in Interrenal Cell Tissue.

By Allan Fraser.

Nature, 1928, **122**, *p.* 206.

In a histological investigation of the interrenal tissue of the ray (*R. clavata*), it has been found that while the majority of the glands examined correspond to the usual description of an ochre-yellow body, a minority show a brown coloration apparently due to melanin pigment. In the yellow glands the lipin has been found to be confined to the cells of the lobules which compose the organ, but in the brown glands a considerable proportion of the lipin lies in the interlobular blood-spaces. The photomicrograph taken from a gland prepared by Marchis' method shows this quite clearly. The black masses of osmicated lipin obviously lie between the lobules. The appearances suggest very strongly that the brown glands when fixed were actively secreting lipin into the blood. The relation between lipin secretion and melanin formation is probably significant.

A. F.

The Effect of Electrolytes on the Muscle of the Fore-gut of *Dytiscus marginalis* with Special Reference to the Action of Potassium.

By A. D. Hobson.

Brit. J. Expt. Biol., 1928, **5**, *pp.* 385–393.

A medium of the composition NaCl 0·161M. : KCl 0·003M. : $CaCl_2$ 0·002M. : pH 7·2 will maintain rhythmic contractions of the striated muscle of the crop of Dytiscus for long periods. In the presence of normal concentrations of sodium the responses to changes of the K or Ca concentration are similar to those described by Hogben and by Wells for other invertebrate muscle preparations. If the concentrations of K and Ca are increased while the K/Ca ratio is kept constant there is decrease in the completeness of relaxation while the rhythm becomes more regular. Complete elimination of sodium from the medium is possible, and the muscle maintains its activity for a long time in presence of potassium and calcium only. Under these conditions the muscle reacts normally to changes in the K/Ca ratio. The optimum K/Ca ratio is about 0·4 which is to be compared with the optimum Na/Ca ratio of 50. A. D. H.

The Action of Isotonic Salt Solutions on the Unfertilised Eggs of *Thalassema neptuni*.

By A. D. Hobson.

Brit. J. Expt. Biol., 1928, **6**, *pp.* 65–78.

At the pH of sea-water isotonic calcium chloride causes artificial parthenogenesis of the eggs of Thalassema. Under the same conditions the chlorides of sodium, lithium, and potassium have no activating power. KCl, in fact, inhibits maturation and quickly renders eggs incapable of being fertilised. Mixtures of $CaCl_2$ with the chloride of an alkali-metal in certain proportions cause parthenogenesis, and, in the case of potassium at least, may be more effective than pure calcium chloride. When the activating power of a series of K+Ca mixtures is tested it is found that there are two optima, one where the calcium concentration is high and one where it is low. If the calcium concentration is low, sodium and lithium seem to be much less effective in causing activation than potassium. The time factor is of great importance. For all activating solutions two optimal times of exposure were found, at 6–9 mins. and at 30 mins. It is concluded that, in Thalassema, cleavage is directly continuous with maturation, and that the difference between a stimulus causing the former and one causing the latter is merely quantitative.

A. D. H.

Observations on the Metabolism of Nervous Tissue.

By E. G. Holmes and B. E. Holmes.

Minerva Medica, 1928, **8**, No. 23 *bis*, *pp.* 1–8, *re-paged reprint.*

Previous work on the metabolism of the mammalian central nervous system is discussed. It is shown that the brain produces lactic acid from added glucose in vitro, and that under the same experimental conditions lactic acid is oxidised. The brain contains but a very small store of carbohydrate, and it is shown that during life it is dependent for lactic acid precursor on sugar supplied by the blood stream, so that the lactic acid value after death depends on the blood sugar level at the time of killing.

Observations on the peripheral nerve show that in contrast to brain this tissue has a carbohydrate reserve which, in anaerobic conditions, is connected to lactic acid. Oxidative removal of lactic acid has not been demonstrated.

Unlike both kinds of medullated mammalian nervous tissue, the non-medullated nerve ganglia of Mia contain large amounts both of glycogen and of free sugar. In vitro, this is slowly converted to lactic acid under anaerobic conditions.

E. G. H.

Entwicklungsgeschichtliche Florideenstudien.

Lunds Universitets Årsskrift, N.F. Avd. **2**, *Bd.* 24, *Nr.* 4, *pp.* 127, 64 fig.

By Harold Kylin.

The following species have been described, with illustrations : *Aghardiella tenera, Asparagopsis hamifera, Atractophora hypnoides, Bonnemaisonia californica, Calliblepharis jubata, Callophyllis obtusifolia, Callymenia reniformis, Catenella opuntia, Chantransia rhipidandra, Chondria dasyphylla, Cruoria pellita, Cumagloia Andersonii, Dudresnaya coccinea, Endocladia muricata, Epilithon membranaceum, Gelidium cartilagineum, Gigartina leptorhynchos, Halarachnion ligulatum, Helminthora divaricata, Iridaea cordata, Laurencia pinnatifida, Naccaria Wigghii, Peyssonnelia Dubyi, Phyllophora membranifolia, Ptilothamnion pluma, Rhodoglossum affine, Ricardia saccata, Stenogramme interrupta.*

W. R. G. A.

The Larval Stages of the Plymouth Brachyura

By M. V. Lebour.

Proc. Zool. Soc., London, 1928, *Pt.* 2. *pp.* 473–560, *Pl.* 16, *Fig.* 5.

This is a survey of all the larval crabs which have been studied in the neighbourhood of Plymouth ; 37 species are known, 33 are described fully or partially, and the relationships of the larvæ discussed. Whenever possible the crab has been hatched from the egg and a coloured drawing made of the first zoea ; 30 zoeæ were thus drawn, 23 of which came from the pre-zoea hatched from the egg. Larvæ of the rarer crabs were obtained from the plankton, also stages of various species when not reared through the complete life-history. Three species have been reared from egg to crab, many others through several stages. Larvæ from the plankton were kept until they became crabs. In this way it has been found possible to distinguish the larvæ of nearly all the Plymouth crabs. Accounts have been given of each species, with reference to the previous work of other authors and keys formed for use of plankton workers. It was found that there were distinct differences between the larvæ of the Oxyrhyncha and the Brachyrhyncha, and in most cases between the genera in both groups. It should now be possible to place any British larval crab in its proper genus if not species. A note on further work on the larval stages of foreign crabs is added. The paper is illustrated by 16 plates, 3 of which are coloured.

M. V. L.

The Food of *Sardina pilchardus* (Walbaum).

By M. V. Lebour.

Bull. Soc. d. Sci. Nat. du Maroc, 1927, **7**, *pp.* 220–223.

This is a very brief account of the food of the sardine from Casablanca, Morocco, from slides of the stomach contents, sent by Monsieur R. Ph. Dollfus. The most frequent food was *Peridinium depressum*, and secondly, the silicoflagellate *Dictyocha fibula*. These were mixed with a variety of diatoms, dinoflagellates and other protista, besides copepods and numerous larval metazoa.

M. V. L.

Brachiella obesa, a Parasitic Copepod of *Trigla Cuculus*, with a Description of the Male.

By W. H. Leigh-Sharpe.

Parasitology, 1928, **20**, *pp.* 25–31.

Brachiella obesa is not uncommon on *Trigla cuculus* at Plymouth in the neighbourhood of the Eddystone. Early in June one fish in ten harboured the parasite (5 : 50), and two of the females bore males. The appendages of the female are described; attention is called to the postero-lateral lobes of the trunk from which issue the egg-sacs, the pateriform bulla, and the striking resemblance of the maxillipedes to those of Ommatokoita. The male with its appendages is described for the first time, and while not resembling in form the more typical males, e.g. *B. thynni*, it bears a close resemblance to the American species *B. gulosa* Wilson. Some remarks on the relationship of Brachiella to other genera are added.

W. H. L.-S.

Note on the Tail-organs of Acetes.

By Yô K. Okada.

Ann. Mag. Nat. Hist., 1928, ser. 10, **1**, *pp.* 308–310.

There are two enigmatic organs in the uropod of *Acetes japonicus*, one in the basal segment and the other in its endopodite. They are visible in the fresh condition as red spots.

The structure is the same in all four; a mass of large plump cells having round nuclei forming the centre of the organ, which is limited by a thin layer of circular fibres and externally is clothed by a thick investment of radial fibres. The colour of the spots is due to the presence of red pigment granules in the outer investment.

The function is unknown, but may be photogenic. Both outer and inner investments are pierced here and there by a number of what are probably blood-capillaries, and the centre of the organ seems to receive an abundant supply of blood.

Y. K. O.

Feeding Organs and Feeding Habits of *Autolytus Edwarsi* St. Joseph.

By Yô K. Okada.

Q.J. Microscop. Sci., 1928, **72**, *pp.* 219–245.

At Plymouth *Autolytus Edwarsi* is always associated with Obelia. The meaning of this association is easily understood as the former lives upon the latter. The Syllid deprives the hydroid of the hydranths and eats them.

The worm cuts off the tentacles from the hydranth with the toothed crown of the chitinous tube, and sucks them up through the protruded pharynx by establishing in the front of the alimentary tract, by the activity of the proventriculus, a continuous water-column, which is drawn back into the intestine.

The pumping action of the proventriculus is particularly strong and distinctly visible at the outset of feeding. After a short time it dies away and the action is followed by peristalsis in the intestine.

The entire organisation in the front part of the alimentary tract, which is the feeding apparatus of the animal, suggests the system of a suction pump, the pharynx representing the pipe, the proventriculus the pump itself with a valve at each entrance, and the ventriculus the regulator of the water-column.

Y. K. O.

The Biology of Shell-fish in Relation to Public Health.

By J. H. Orton.

J. Roy. Sanitary Inst., 1928, **49**, (5), *pp.* 263–274.

In this communication is reproduced an address given to Section E, Hygiene of Food, at the Congress of the Royal Sanitary Institute at Plymouth, July, 1928.

The general structure of bivalves was illustrated by a wooden model, shown in the drawing in Fig. 1, and habits, habitats, modes of feeding, breathing and reproducing along with the incidence of disease and death were reviewed in relation to the production of pure and polluted animals.

Pollution and purification were discussed briefly, and it was shown that

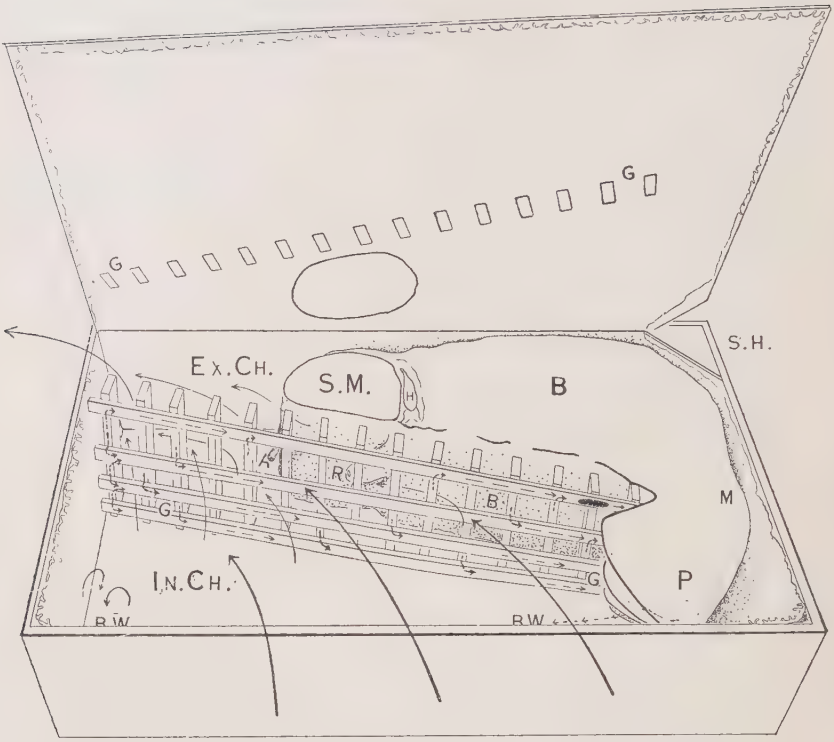

FIG. 1.—A box model of the generalised construction of a bivalve shell-fish to show essentially the division of the shell-space into two main compartments by the gill (G.G.),which is in principle a grid-like sieve. The cut edges of the vertical gill-bars and the shell-closing muscle are shown both in the lower and upper valves, which are represented by the box and its lid. One main compartment contains the body (B), the shell-closing muscle (S.M.), and the exhalent chamber (Ex.Ch.), while the other, lower compartment is composed entirely of the inhalent chamber (In.Ch.) and also contains the lip-folds or palps (P.).

G.G. The grid-like gill consists essentially of numerous vertical gill-bars and four horizontal main food channels, and hangs like a curtain between the inhalent and exhalent chambers. Sets of cilia on the gill both maintain the current of water through the gill-spaces and the shell-chambers, and sieve off the food-particles brought into the shell in this current of water. Food-particles are collected on the front faces of the vertical gill-bars and transported thence (as shown by the small broken-line arrows) into the main horizontal food channels. In these latter channels food masses or particles are carried along towards the mouth (as indicated by the larger broken-line arrows). One food-mass is shown approaching the palps in the uppermost food channel.

A. Anus and rectum in the exhalent chamber.

R. Combined renal and reproductive aperture (of the right side), which also opens into the exhalent chamber.

B.W. Back-waters in the inhalent chamber in which rejected food or other unwanted material is collected and from which such material is periodically expelled.

a consideration of the biology of bivalves leads to a recognition of the following cardinal facts :—

a. Any solid impurities which may occur in the water must necessarily be taken from the water and at least arrested on the body of the animal.

b. Bivalves are in the best condition as a food product in the fattening and pre-spawning periods of their life-history ; and in the worst condition in the spawning and post-spawning periods.

Therefore from the point of view of Public Health the following conclusions may be drawn :—

1. The indiscriminate consumption (especially in the uncooked state) during summer of those bivalves, whose spawning or post-spawning periods occur in summer, is in most cases inadvisable, if such shell-fish originate from estuarine beds.

2. There is a need for a clearly defined and recognised standard of purity in bivalves, or alternatively, the beds or other situation from which the bivalves are taken for consumption.

3. Existing beds of bivalves should be reclassified under recognised standards of purity.

J. H. O.

Contributions to the Cytology of Tetrasporic Plants of *Rhodymenia palmata* (L.) Grev., and some other Florideæ.

By M. A. Westbrook.

Ann. Bot., 1928, 42, *pp.* 149–172, Pls. II and 8 figs.

Somatic division is illustrated and described in detail for tetrasporic plants of *Laurencia pinnatifida* (Gmel.) Lamour., *Chondria dasyphylla* (Woodw.) C. Ag., and *Rhodymenia palmata* (L.) Grev., and compared with that in others of the Florideæ. Common features are the small nuclei, the large number of small chromosomes, and the absence of a spireme stage.

Stages in the prophase of the first division of the tetrasporangium are described for *Laurencia pinnatifida*, *L. hybrida* (D.C.) Lenorm., *Chondria dasyphylla*, *Stenogramme interrupta* (Ag.) Mont., and *Rhodymenia palmata*. For all but *Stenogramme* spireme stages are figured and evidence adduced for the occurrence of meiosis. In the tetrasporangia of *R. palmata* a peculiar stage is described and compared with the " growth period " of some animal oocytes, where the nucleus, after developing a spireme, returns to an apparently resting stage. A process of regeneration of the tetrasporangium is reported for *R. palmata*.

Attention is drawn to the anomalous life-history of the latter. Up to

the present only male and tetrasporic plants have been found, but the cytological results here recorded are taken to indicate that there is a nuclear fusion in the life-cycle. The possible occurrence of as yet unidentified female plants is suggested.

M. A. W.

Note on a Method of Obtaining Long Working Distances with Low-power Objectives.

By Douglas P. Wilson.

J. Roy. Microscop. Soc., 1927, **47**, *pp.* 335–337.

A 2-in. or $1\frac{1}{2}$-in. objective screwed on to the nosepiece of the microscope in the usual way is used in conjunction with a $\frac{2}{3}$-in. objective which is screwed on to the lower end of the draw-tube. An eyepiece is in the usual place. By sliding the draw-tube in and out and so varying the distance between the two objectives it is possible to focus and considerably magnify small objects at a fair distance from the microscope. The same combination can also be used as a telescope.

D. P. W.

Notices of Books.

Biological Chemistry and Physics of Sea-Water. By H. W. Harvey, M.A., Hydrographer at the Laboratory of the Marine Biological Association, Plymouth. Cambridge University Press, pp. 194, 1928, 10s. 6d. net.

Of biological chemistry, as ordinarily understood, the book is quite innocent, but it does give a very readable account of the biological relations of the chemistry and physics of sea-water. There is no padding, and the pages are packed with relevant quantitative data, including many culled from the author's own researches—from which one may correctly infer that it is no mere compilation.

It contains the author's simplified presentation of Bjerknes' circulation theory, here published for the first time, so that the non-mathematical can comprehend it. The book should have many readers outside the narrow circle of marine biologists.

W. R. G. A.

Birds of the Ocean. A Handbook for Voyagers, containing descriptions of all the sea-birds of the world, with notes on their habits and guides to their identification. By W. B. Alexander, M.A. G. P. Putnam's Sons, The Knickerbocker Press, pp. 428, 1928, 15s. net.

In this handy-sized volume Mr. Alexander has produced a work from which it should be possible for any ocean voyager to identify sea-birds that may be seen from the deck of a ship. The book is copiously illustrated with excellent photographs of many of the birds, with an additional series of half-tone illustrations from drawings made by the author to illustrate the main features for identification of birds while on the wing, or, in the case of Penguins, Auks and Phalaropes, on the water. The birds are treated in their families, with a short general description of the habits of each family; the families have been subdivided into groups based on size and colouring, with keys by which the birds observed may be readily narrowed down to the groups in which they occur, the identification being then possible from the individual descriptions of each species within the group.

The book should be helpful in affording an interest to vary the monotony of sea voyages, and should be no less useful for the identification of the many birds to be seen by shore ramblers in various parts of the world.

F. S. R.

Life in Inland Waters, with especial reference to Animals. By Kathleen E. Carpenter. Sidgwick & Jackson, Ltd., 267 pp. 1928.

This work constitutes a further addition to the list of text-books of animal biology edited by Professor Julian S. Huxley.

No British book has yet appeared dealing with the subject of freshwater biology as a whole, and Miss Carpenter has therefore filled a long-felt need. The book covers a wide field, dealing first with the general characteristics and habits of the freshwater fauna and the medium in which they live; and in the latter half of the work with the ecology of freshwater life, devoting a chapter to each of the various types of environment, such as head-streams, rivers, lakes and small water bodies.

The attention of British workers has largely been turned to Marine Biology owing to the greater wealth of animal types in the sea and its larger economic importance. Nevertheless, fresh-water biology has its economic view-points, notably in the problem of pollution and its effect on the fisheries and the water supply for our great cities.

With its helpful list of references at the end of each chapter, this book should stimulate students to further research, and, not the least important, as pointed out both by the author and editor, should help to foster that love of nature which should be inherent in all engaged in biological research.

F. S. R.

Queer Fish: Essays on Marine Science and other Aspects of Biology. By C. M. Yonge, D.Sc., Ph.D. George Routledge & Sons, Ltd., pp. 193. 1928.

In this book, in the "Science for You" series, Dr. Yonge has collected together a number of articles, most of which have already appeared in print in various periodicals. Two-thirds of the book are devoted to marine biology and our sea fisheries, stressing the importance of the resources available for mankind and the consequent need for research. Necessarily from the nature of the book the subject is not treated exhaustively, being merely a collection of essays treating marine biology and interesting items of research in an easy and popular manner.

The remaining pages comprise a set of articles on various aspects of biology, such as heredity, tissue culture and ecology.

The book can be thoroughly recommended as containing a number of interesting essays, each one of which supplies accurate information that makes light reading, but should not be regarded as producing a consecutive whole.

F. S. R.

Science of the Sea : an Elementary Handbook of Practical Occanography for Travellers, Sailors and Yachtsmen. Prepared by The Challenger Society for the Promotion of the Study of Oceanography. Originally edited by G. Herbert Fowler, B.A. Ph.D. Second edition, edited by E. J. Allen, D.Sc., F.R.S. Oxford University Press, 1928. 15s. net.

The Challenger Society have prepared a second edition of their handbook *The Science of the Sea*, originally published in 1912, which has been re-edited by Dr. Allen. The work has been very largely revised, many of the chapters having been entirely rewritten. Of new authors who took no part in the original edition are Mr. D. Brunt and Commander Garbett, who have written the chapter on the air ; Dr. W. R. G. Atkins, who contributes an article on the alkalinity of sea-water ; and Dr. M. V. Lebour, who deals with the floating plants. Most of the original illustrations are reproduced with the addition of a few new ones, while the general format of the book is a vast improvement on that of the first edition.

This book should be in the library of all interested in the science of the sea, and especially of naval officers and the owners of yachts, who wish, while enjoying the pleasures of sea voyaging, to contribute something, however small, to our knowledge of life in the sea. The criticism may be made that in such a volume the study of marine life appears too formidable for a leisure hour, but really in its comprehensive nature lies its advantage, for a taste in any individual direction is catered for, and with a wise use of the book much can be achieved in the study of some special problem or group of organisms in out-of-the-way parts of the world.

F. S. R.

The Seas, our Knowledge of Life in the Sea and how it is Gained. By F. S. Russell, D.S.C., B.A. (Cantab.), Assistant Naturalist to the Marine Biological Association, Plymouth, and C. M. Yonge, D.Sc., Ph.D., Leader of the Great Barrier Reef Expedition, 1928–9. 379 pp., with 384 illustrations, 167 of which are in full colour. Frederick Warne & Co., London, 1928. 12s. 6d. net.

This book is beautifully illustrated, and the text contains accurate information on many of the main lines along which marine research is progressing. The subject is so wide that even those who are specialists in one or more of its branches are likely to find material that is new to them ; this is served up in a palatable form with little or no loss in exactness. This characteristic differentiates the book from many others of a popular type—yet as a popular exposition of the subject it appears to have very considerable merit.

W. R. G. A.

Marine Biological Association of the United Kingdom.

Report of the Council, 1928.

The Council and Officers.

Four meetings of the Council have been held, at which the average attendance has been seventeen. These meetings were held in the Rooms of the Royal Society, and the thanks of the Council are due to the President and Council of the Society for this hospitality.

A Committee of nine members of the Council visited and inspected the Plymouth Laboratory, and the scientific work which was being carried on.

The Council has to report with regret the death of Mr. W. T. Brand, who had been a Governor of the Association, representing the Fishmongers' Company, for a number of years.

The Plymouth Laboratory.

The Laboratory buildings have been maintained in good condition. New ventilators of the Boyle type have been fixed above the main Laboratory, the outside painting of the old building has been carried out, and a certain amount of distempering and painting has been done inside. The cement work of the new building has been coated with a special preparation to keep out damp.

The equipment for biological and chemical work is good, save as regards the supply of some of the more costly instruments, such as polarimeter, refractometer, spectrophotometer and binocular dissecting microscopes, which are necessary for certain types of work. The supply of physical apparatus is being increased as funds permit, and it is of interest to note that various instruments, purchased as being of general utility, have all been used within the year.

The engines and pumps, circulating sea-water through the Aquarium and Laboratory tanks, have run without requiring heavy repairs. A small independent circulation, worked by an electric motor and

centrifugal pump, has been installed in the new building, and has proved a valuable addition to the equipment.

A new electrical air-blower has been bought, which gives an independent supply of compressed air to the Aquarium and laboratories.

At Pier Cellars, Cawsand Bay, a sea-wall of reinforced concrete has been built across the mouth of the cove, so as to enclose a sea-water pond. This work has been done, with a special grant from the Ministry of Fisheries, for the purpose of carrying out certain experiments on the growth of Plaice, which are required by the Ministry in connection with their own work.

The Ship and Motor Boat.

The steam drifter *Salpa* and the 25 ft. motor boat have worked continuously throughout the year, in both cases at a low cost of maintenance. The ordinary surveys and refits have been carried out, and both vessels are in good order.

The Staff.

Mr. C. F. A. Pantin was again given leave of absence for some weeks in the early part of the year to enable him to repeat his course of lectures and practical work on Comparative Physiology at University College, London.

Mr. F. S. Russell, who has been lent for nine months to the Great Barrier Reef Expedition, left the Laboratory for Australia at the end of May. Early reports of the work of this expedition, which is under the leadership of Dr. C. M. Yonge, a former member of our staff, are very satisfactory.

Mr. E. Percival, Lecturer on Zoology in the University of Leeds, was appointed a temporary naturalist on the staff of the Laboratory, to take Mr. Russell's place whilst he was away. The Council desire to acknowledge their very great indebtedness to the University of Leeds for allowing Mr. Percival the leave of absence necessary for him to take up work at Plymouth. As will be described later, Mr. Percival has undertaken a special investigation of the fauna of the estuaries in the Plymouth district. The Council wish to congratulate him on his appointment to the Zoology Professorship at Christchurch, New Zealand.

Mr. D. P. Wilson, after holding a student-probationership at the Laboratory for six months, was appointed in April an Assistant Naturalist on the staff.

Mr. H. O. Bull, who for two years was a student-probationer, was appointed a research assistant to conduct the Plaice experiments at Cawsand Bay. After organising the work there he received an appoint-

ment as Naturalist at the Dove Marine Laboratory, Cullercoats. Mr. B. Dawes, of the Imperial College of Science, was appointed to take charge at Cawsand, and commenced work there in August.

Mr. V. C. Wynne-Edwards, of Oxford, and Mr. G. A. Steven, of Edinburgh, have been appointed student-probationers.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year :—

Dr. W. R. Amberson, London and Philadelphia (General Physiology).
C. Amirthalingam, London and Ceylon (*Pecten operculatis*).
Miss D. Atkins, London (Pinnotheres and Loxosoma).
W. A. Bain, Edinburgh (Physiology of the Crustacean heart).
L. E. Bayliss, London (Pecten muscle).
N. J. Berrill, Leeds (Hatching enzymes in Ascidians).
Miss A. Bidder, Cambridge (Regeneration of Sponges. Digestion in Loligo).
Dr. H. Boschma, Utrecht (Oceanography).
Prof. J. P. Bouckaert, Louvain (Crustacean nerve).
E. Boyland, Manchester (Physiology of Pecten muscle).
Dr. E. Bozler, Munich (Physiology of the adductor muscle of Pecten).
Miss G. T. Brock, Oxford and Cape Town (Abnormal tails in young herring).
Miss E. M. Brown, London (Physical and chemical effects on Sea Urchins. Development of Sagartia).
F. S. Callow, London (Heterogonic growth in Eupagurus).
Dr. J. D. S. Cameron, Edinburgh (Renal excretion of urea).
A. Candeias, Lisbon (Oceanography).
Prof. H. Graham Cannon, Sheffield (Crustacean feeding mechanisms).
Mrs. H. Graham Cannon, Sheffield (Anatomy of *Amphitrite Johnstoni*).
Dr. H. H. Darby, New York (H ion concentration in relation to protozoan development).
Mrs. H. H. Darby, New York (Chemistry of Sea-water).
A. C. Downing, London (Adjusting Downing Galvanometer).
Prof. H. Dryerre, Edinburgh (The cardio-inhibitory fibres of Dogfish).
P. Eggleton, London (Chemistry of muscles of *Raia clavata*).
Mrs. P. Eggleton, London (Chemistry of muscles of *Raia clavata*).
Miss G. H. Faulkner, London (Chromosomes of Obelia. Heteronereis of Leptonereis).
A. Fraser, Aberdeen (Inter-renal cell tissue of Elasmobranchs).
K. Furusawa, London and Japan (Non-medullated nerve).
P. A. Gorer, London (Crustacean inhibitory nerves).
A. Graham, Edinburgh (Digestion in Solen and Holothuria).
Miss A. Hastings, London (Polyzoan larvæ).
H. R. Hewer, London (Colour patterns of Pleuronectidæ).
Prof. A. V. Hill, F.R.S., London (Muscle physiology).
A. D. Hobson, Edinburgh (Artificial parthenogenesis in Echinoderms and Annelids).
Dr. R. Izumi, Japan (Herring larvæ).
P. Kirtisinghe, London and Ceylon (Enteric plexus in fish).
Miss F. M. C. Leak, Sheffield (Antennal gland of Decapods. Euphausids).

M. W. De Laubenfels, California (Cellular behaviour, using Sponges).
Dr. A. Meyer, Prag (1. Cœlomic ciliary circulation in Vermes. 2. Nephridia and genital ducts in Polychæta).
Miss G. L. Naylor, Plymouth (Marsh Fucoids).
Miss E. A. Nicol, Edinburgh (Physiology of digestion in Sabella).
Dr. Yô K. Okada, Tokio (Regeneration in Autolytus and other Polychætes).
G. W. Otter, Cambridge (General Zoology).
R. Palmer, London (Effect of fixatives on the isoelectric point of basichromatin).
E. Percival, Leeds (Estuarine fauna of Rivers Tamar and Lynher).
Sister Philippa and Sister Rose Julie, Liverpool (General).
Mrs. K. F. Pinhey, Montreal (Hæmocyanin. Tyrosinase in Crustacea).
Dr. H. H. Poole, Dublin (Penetration of Light into Sea-water).
Miss R. Renton, London (Physical and chemical effects on Sea Urchins. Development of Sagartia).
H. Roy, London and Calcutta (Protozoology).
S. B. Setna, Cambridge and Madras (Histology of Lamellibranch gill).
Miss E. M. Singer, London (Physiology).
H. S. Soliman, London and Cairo (General Zoology).
Dr. K. M. Ström, Oslo (Estimation of phosphates, silicates and nitrates in sea-water).
Miss W. J. Wadge, Leeds (Effect of alterations in ionic concentration on muscular contraction).
Prof. D. M. S. Watson, F.R.S., London (General Zoology).
Miss K. Weeks, Southampton (Water vascular system of Holothuria).
S. M. White, Manchester (Nerves of fishes).
Dr. C. M. Yonge, Cambridge (Absorption in Lamellibranchs).
Dr. J. M. Yoffey, Manchester (Investigation of hæmoporesis in fishes, and the fundamentals of the splenic circulation).

The usual Easter Vacation Course in Marine Zoology was conducted by Dr. J. H. Orton, and was attended by forty-one students from Oxford, Cambridge, London, Edinburgh, Birmingham, Sheffield, Reading, and Holt.

An advanced Course in Comparative Physiology and Experimental Biology, conducted by Mr. C. F. A. Pantin, was held during the Summer Vacation and attended by twelve students.

During the Easter Vacation Dr. E. W. Shann brought a class of five boys from Rugby, Mr. J. M. Branfoot a class of six from Oundle, Mr. D. M. Reid one boy from Harrow, Mr. A. S. Gillespie a class of five from Monkton Combe School (Bath), and one boy from Caterham.

During Whitsuntide Mr. W. H. Leigh-Sharpe brought a class of five students from Chelsea Polytechnic.

General Work at the Plymouth Laboratory.

The study of the herring and its fisheries in the English Channel and off the south-east of Ireland has been continued by Mr. Ford, and four papers have been published dealing with different parts of the work,

which are either completed or still in hand. Special attention has been devoted to the collection and examination of young herrings, in their first year of life, from several localities. As stated in last year's Report, sampling with a small-meshed seine in the rivers Tamar and Lynher was commenced on May 26th, 1927. As the result of this somewhat late start, the main period of metamorphosis was missed in that year. The sampling thus commenced was, however, continued regularly until July, 1928, and the highly important events occurring annually in the spring months were observed with precision in the spring of 1928. It is now possible to give an account of the general features of the growth of young herrings in these rivers from the transparent pre-metamorphosis stage, until they are fully scaled fishes one year old.

The small-meshed seine has also been successfully used in the rivers Dart and Fal, as well as off the beach at Pentewan on the Cornish coast, and excellent hauls of young herrings, sprats and pilchards obtained. It was a matter of some surprise to find that "whitebait" herrings caught off Pentewan on July 25th, 1928, where the water was made "milky" and opaque with an outflow of freshened water carrying china-clay waste, were literally gorged with the larvæ and pupæ of Chironomid flies.

The progress of the Plymouth winter fishery for herrings during the season 1927–28 was watched and samples of the fishes landed were examined for length, age and sexual condition. The total quantity of fish landed constituted a record for the port, in spite of a marked reduction in the number of vessels participating in the fishery. The average price per 1 cwt. realised on the market, on the other hand, fell to pre-war level. The records of age of the herrings, as indicated by the scales, gave evidence that "3 zoned 3 ringed" fishes were relatively much more heavily represented than in preceding seasons; in other words, fishes of the year-class 1925, which had become large enough to be caught in appreciable numbers probably for the first time during the season 1927–28, were unusually numerous. It would seem, therefore, that this year-class is destined to become an important constituent of the landings during seasons of the near future.

In accordance with the programme of work outlined in the last Report, Dr. Orton has given as much time as possible to preparing earlier work for publication. Attempts were made to examine samples of oysters at times critical for shell-growth (shell-shoots), but he finds it now difficult to obtain material regularly from the beds formerly studied, owing largely to their depleted state. A few observations were made on rapidly induced summer shell-growth (shell-shoots), in a pond at the River Yealm.

Some observations on growth, breeding, sex, and shell-shape in Patella

have been prepared for publication. Parts I and II of this work are published in Vol. XV, 3, of the Journal; Part III, concerning shell-shape, called for further field-work, and is approaching completion. The variation in shell-shape in Patella, in relation to environmental conditions, is a subject of much interest, as the animal is semi-sedentary and periodically visible, while there is great diversity of statement in the literature as to the distribution, cause, and the extent of this variation. An attempt is being made to express the variations numerically, and to discover the underlying cause or causes of the variations observed. It has been found that Limpets which are covered at neap tides have low and light shells, while those growing above high-water neaps have relatively high and heavy shells, which are higher and heavier (thicker) in the drier than in the damper localities. At least two different growth-forms occur at successive ages in some—and probably all—environments, and these are somewhat different in different environments; therefore differential growth-rates are themselves subject to variation. There is a definite relation between the mean axis of the shell and weight.

In this work it has been found that the habits imposed upon the animal by environmental conditions offer a simple explanation, which can be tested experimentally, of the variation in shell-shape. A similar deduction was made regarding shell-shape in the oyster, and Dr. Orton considers that there is ground for applying the simple relation between habit and variation in shape in different types of animals. In Patella and the oyster, the thickness—and some other characters—of the shell would appear to be more directly related than shell-shape to natural environmental conditions, i.e., they are physiological effects independent of habits. A correlation between intensity of light or radiant heat and thickness of shell is suspected.

In continuing his experiments on whelk-tingles, Dr. Orton, with Mr. Winckworth, has found that on the Blackwater oyster beds, in addition to *Purpura lapillus* and *Ocenebra erinacea* (=Murex), there also occurs *Urosalpinx cinerea*. The latter is the American oyster-drill pest, which has undoubtedly been introduced into English waters, in the same way as *Crepidula fornicata*, on American oysters, and has previously escaped notice. Among 1672 tingles dredged in autumn only 5·4% were Urosalpinx, whereas in summer almost pure catches of this pest can be taken on oyster layings at low water, where these animals congregate to spawn and feed. Long-standing experiments with rather small Plymouth-born Ocenebra have so far failed to show that individuals of this species, which have never seen oysters, can recognise them as prey, although large Fal Ocenebra rapidly devour oysters from the Blackwater, but also eat barnacles.

Dr. Orton read a paper before the Royal Sanitary Congress at Plymouth

on "The Biology of Shell-fish in relation to Public Health" (published in the Journal of that body, November, 1928), and one before the Challenger Society at Conway on "The Oyster as a Biological Subject."

The continuous record of hydrographic data between Plymouth and Ushant, commenced in April, 1921, has been maintained, the observations having been made by Dr. Atkins and Mr. Harvey, the data being sent to the French Fishery Department for publication in the Rapport Atlantique of the International Council. Mr. Harvey has continued investigations on the technique of determination of nitrates in the sea, with the aim of further developing and simplifying the method, so that it can be carried out on board ship with maximum accuracy. There is a demand by workers in other countries for a source of supply of the necessary reagent, the manufacture of which presents difficulties, and research in connection with this is in progress. An attempt was also made to develop a method of colour comparison, in order that the determination of small quantities of phosphate and of silicate in sea-water may be carried out with less eye-strain, with less delicate colour perception on the part of the observer, and if necessary in artificial light. A communication on these subjects and demonstrations were given at the Scientific Meeting of the International Council at Copenhagen in June. Mr. Harvey was then asked to spend October at Professor Hjort's laboratory at Oslo to collaborate with delegates from Norway, Germany and Finland in investigating the possibilities of simplifying the methods and the limitations of their application, and in drawing up recommendations for the technique of carrying out the estimations of nutrient salts in sea-water. These recommendations are being published as an appendix to the Rapports et Procès Verbaux of the Scientific Meeting of the International Council and are being communicated to the American, Danish and Dutch Expeditions, which are now at sea or shortly leaving, and include a survey of the available nutrient salts in the oceans in their scientific programmes. The development and provision for manufacture of an apparatus for colour comparison in the estimation of phosphates, embodying the principles of the apparatus evolved in the Plymouth Laboratory and used at Oslo, is being undertaken by Dr. H. Wattenburg of the *Meteor* expedition.

In view of the increasing number of workers who are employing the methods evolved at Plymouth for estimating the available nutrient salts in the sea and mapping their distribution over wide areas, it is advisable that the methods be reduced to as simple a technique as possible, and that the personal equation in colour comparison be reduced to a minimum. Much work remains to be done on the rate of re-formation of nitrate from dead organisms, on the possible direct utilisation of ammonia by

phytoplankton and on the rate of diffusion upwards of nutrient salts into the depleted upper layers.

Mr. Harvey has also been engaged upon a simple method for calculating those currents which give rise to, or are maintained by, an unequal distribution of density in the sea. A communication on the hydrodynamics of the waters south-east of Ireland, embodying this method, will shortly be published.

Dr. Lebour has finished her account of the larvæ of the crabs of the Plymouth area (with the exception of a few rare forms). This has now been published in the Proceedings of the Zoological Society (July, 1928), in a paper entitled, "The Larval Stages of the Plymouth Brachyura." She has also completed her book on "The Planktonic Diatoms of Northern Seas," on the same lines as her "Dinoflagellates of Northern Seas." The Royal Society has granted £75 towards the expenses of its publication, and the Ray Society has accepted it to issue to its subscribers for 1929. She is also studying various planktonic larvæ and has distinguished those of the two species of Alpheus, *Alpheus macrocheles* having been hatched from the egg.

Dr. Lebour is now engaged upon a revision of the account of the Plymouth Marine Fauna, which has been out of print for several years. This account contains records of the positions in which each species has been found in the local area, as well as the available information as to breeding seasons.

During the early part of the year, before his departure for Australia, Mr. F. S. Russell continued his studies on the vertical distribution of young fishes and other plankton organisms. Papers have been published in the Journal dealing with the rise and fall in the water of the Copepod, *Calanus finmarchicus*, and with similar movements of young fishes. These movements have been analysed and discussed in connection with variations of the different physical conditions in which the animals live.

Mr. E. Percival spent the six months, June to November, in making and examining collections from the fauna of the River Tamar and the St. Germans River (Lynher). The regions above the junction of the two rivers were studied chiefly, but St. John's Lake, nearer the sea, was also visited. The salinity of water samples from various places was determined and an attempt made to correlate salinity and faunistic changes. It was noticed that a relatively sudden reduction in number of marine species, especially of the plankton, took place where the salinity began rapidly to fall, that some of the marine littoral species can withstand a much greater range of salinity variation than can others, and that brackish-water species also do not appear all to have the same ability to suffer similar salinity changes.

Neomysis vulgaris, *Gobius microps* and *Eurytemora affinis* were found

to have the greatest ranges, persisting almost into fresh-water. An interesting succession of species was observed, in which a group of forms was succeeded, in the less saline region, by a group of closely related brackish-water species.

The brackish-water possesses a very much less varied fauna than the estuarine or harbour waters, and the apparently fresh-water region at the upper end of the tidal area has a scanty population in which figure fresh and brackish-water species. The most numerous organisms were found to be three Mysids, two Calanids, *Nereis diversicolor*, four *Polyzoa* and *Gobius microps*. The fauna is very dense in some places, especially at the edge of the tide. Over 160 species have been recorded, some being additions to the list of the Plymouth area.

Mrs. E. W. Sexton's investigations on Mendelian inheritance in *Gammarus chevreuxi*, in which she has been assisted by Miss A. R. Clark, have made progress, more especially in connection with the study of a mutation of eye-colour, which has been named "purple-white." In connection with this work, a series of experiments on the effect of temperature on the rate of development of the eggs has been completed, and the results are to be published in the immediate future. A paper by Mrs. Sexton, giving a general account of the rearing and breeding of Gammarus in Laboratory conditions, was published in the Journal during the year.

Mr. H. O. Bull's work on the formation of conditioned "responses" in fishes was described in last year's Report. The detailed paper dealing with it was published in the Journal of the Association in April, and both its scientific value and its general interest have been recognised. After completing this paper Mr. Bull became responsible for organising experiments on the growth of plaice in the sea-pond, which had been constructed at Pier Cellars, Cawsand Bay. The object of these experiments is to ascertain the relation between growth and the amount of food taken by the fishes under investigation, and particularly to determine what proportion is used for maintenance and what for growth, as measured by increase of weight. The preliminary experiments have given interesting results, and have furnished indications as to the lines upon which the work must be continued.

Mr. B. Dawes now has charge of these investigations, which it is hoped to continue during the coming year.

Mr. D. P. Wilson has been continuing his studies on larval Polychætes, and after several attempts, has this year been successful in rearing both *Sabellaria alveolata* and *S. spinulosa* from the fertilised egg right through the metamorphosis, and in the case of the former species has watched the building of the first sandy tube. Many attempts have been made to obtain artificial fertilisations of a number of Polychætes whose larvæ have not yet been described, but only in the case of *Audouinia tentaculata*

and *Notomastus latericeus* was success obtained. In both these cases the pelagic life is comparatively short and the larvæ soon lose their cilia and take to creeping on the bottom.

A study of the development of the Mitraria larva of *Owenia fusiformis* has also been commenced, and this promises to be of special interest. Artificial fertilisations have been made, and twice, out of many attempts, the larvæ have been reared through their metamorphosis and have made tubes in which they have lived and grown for some considerable time. The fully developed Mitraria larva is in many ways a remarkable creature, which at the right time suddenly undergoes a cataclysmic metamorphosis, which may take no more than a few seconds to turn it into a tiny worm, busily engaged in swallowing its cast-off prototroch and other larval structures. There is a great deal in the development, however, which is still obscure and which will necessitate a considerable amount of future work to elucidate.

Mr. V. C. Wynne-Edwards has commenced a study, which is really a continuation of earlier work done at the Laboratory, on the distribution of young fishes in the western end of the Channel. He is making special attempts to follow the growth of young mackerel.

Mr. G. A. Steven is making a detailed study of the fauna of certain definite fishing areas, and is attempting to correlate the results with observations on the food actually eaten by the fishes caught in these areas. Varied methods of collecting are being used, with a view to making the records as complete as possible, and, wherever possible, quantitative estimations are undertaken.

Department of General Physiology.

Dr. Atkins and Dr. H. H. Poole have continued their collaboration on photo-electric photometers, which have been used on the *Salpa* throughout the year ; the initial testing and standardisation was carried out in the laboratories of the Royal Dublin Society. Use was made of the more frequent visits to Station E 1, necessitated by the photo-electric work, to prosecute the investigations of the minor constituents of sea-water at shorter intervals, for it has now been recognised that at certain seasons the changes may proceed with great rapidity. It has become impossible, however, for Dr. Atkins to keep pace with the analytical work involved, if this is to be done on water samples not vitiated by storage. Each new constituent studied means the abandonment of the study of the seasonal changes in another one, and so the whole picture cannot be obtained simultaneously.

Work on the preservations of fishing-nets was also continued upon the samples already treated, but it was not possible to devote any additional

attention to the subject. The routine tensile tests were faithfully carried out by the Laboratory assistant, Albert Ford, whose untimely and sudden death in September, at the age of twenty, was much deplored by the Laboratory.

Mr. Pantin has completed an investigation of the rôle of oxidation in amœboid movement. Under truly anaerobic conditions movement gradually falls in value, until ultimately it ceases abruptly. Oxygen is then required for recovery. Amœboid movement therefore resembles muscle in that the primary process of contraction is anaerobic, oxygen being required only for recovery. Extensive quantitative experiments have been performed on the relation of the velocity to duration of anaerobiosis. Analysis of these results in terms of various hypotheses shows that the experimental facts are in close agreement with only one hypothesis ; that the controlling factor in the mechanism of movement is the rate of change of sol$\rightleftarrows$gel in the protoplasm, and that the anaerobic decay of movement is due to the accumulation of some reaction product (such as lactic acid), which progressively alters the physical state of the protoplasm. The relation of this to muscle physiology is therefore exceedingly close.

Recovery from anaerobiosis is rapid. The relation between the time required for recovery and the period of anaerobiosis indicates that a considerable oxygen debt may be accumulated by the anaerobic amœba. Important conclusions can be drawn from this and are discussed in a forthcoming paper.

In a second series of researches the relation of the velocity of movement to the external oxygen pressure has been investigated. A critical pressure of about 30 mm. of oxygen exists, above which the amœbæ remain normal indefinitely; below this increasing effects are observed, gradually approaching those of anaerobiosis.

Analysis of these results suggests that there exists a *dynamically* dissociable oxidation system in the protoplasm. Reasons are given for supposing this to be connected with the oxidase-cytochrome system of Keilin.

A third series of experiments was carried out to investigate this. The action of cyanide, sulphuretted hydrogen, alcohols and anæsthetics was studied. The results leave every reason to suppose that the oxidative recovery mechanism involves a mechanism similar to or identical with the oxidase-cytochrome system.

The Library.

A special Committee was appointed in March to consider the Library. This Committee reported that the available space for shelves had become very restricted, and that the construction of a further Library building

would be imperative within the next few years. They also pointed out that the cost of the necessary scientific journals now taken was increasing rapidly, and that other very desirable new journals were being published, which could not be purchased out of the funds at present allotted for Library expenditure.

The thanks of the Association are again due to numerous Foreign Government Departments, and to Universities and other Institutions at home and abroad, for copies of books and current numbers of periodicals presented to the Library or received in exchange for the Journal. Thanks are also due to those authors who have sent reprints of their papers.

Published Memoirs.

The following papers, the outcome of work done at the Laboratory, have been published elsewhere than in the *Journal* of the Association.

Atkins, W. R. G. *Lecture Experiments on the Hydrogen Ion Concentration Changes in the Rusting of Iron.* "Nature," Vol. CXXI, 1928, p. 615.

Boyland, E. *Chemical Changes in Muscle, Parts II–III.* Biochem. Journ., Vol. XXII., 1928, pp. 362–380.

Channon, H. J. *The Biological Significance of the Unsaponifiable Matter of Oils. III. Fish-Liver Oils.* Biochem. Journ., Vol. XXII, 1928, pp. 51–59.

Eggleton, P., and Eggleton, G. P. *Further Observations on Phosphagen.* Journ. Phys., Vol. LXV, 1928, pp. 15–24.

Fraenkel, G. *Über den Auslösungsreiz des Umdrehreflexes bei Seesternen und Schlangensternen.* Zeitschr. f. vergl. Phys., Bd. VII, 1928, pp. 365–378.

Fraser, A. *Brown Coloration in Interrenal Cell Tissue.* "Nature," Vol. CXXII, 1928, p. 206.

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Finance.

The Council wish to express their gratitude to the Development Commissioners for their continued support of the work of the Association. They have to thank, also, for generous grants the Fishmongers' Company (£600), the British Association (£50), the Royal Society (£30), the Physiological Society (£30), the Ray Lankester Trustees (£20), the Universities of Oxford (£52 10s.), Cambridge (£105), London (£52 10s.), Bristol, Birmingham, Leeds, Manchester, Sheffield and the Imperial College of Science.

Vice-Presidents, Officers and Council.

The following is the list of gentlemen proposed by the Council for election for the year 1929–30 :—

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Sir E. Ray Lankester, K.C.B., LL.D., F.R.S.

Vice-Presidents.

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Sir Sidney Harmer, K.B.E., F.R.S. (Royal Society).

List of Annual Subscriptions

Paid during the Year, 1st April, 1928, to 31st March, 1929.

	£	s.	d.
Dr. W. M. Aders	1	1	0
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Dr. D. R. Crofts	1	1	0
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Carried forward	48	6	0

	£	s.	d.
Brought forward	48	6	0
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Carried forward	96	12	0

	£	s.	d.
Brought forward	96	12	0
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R. Palmer, Esq.	1	1	0
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	£	s.	d.
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List of Composition Fees

Paid during the Year, 1st April, 1928, to 31st March, 1929.

	£	s.	d.
L. E. Bayliss, Esq.	15	15	0
Prof. R. R. Gates	15	15	0
E. R. Gunther, Esq.	15	15	0
Miss S. M. Manton	15	15	0
G. W. Otter, Esq.	15	15	0
Total	£78	15	0

List of Donations to the General Fund

For the Year, 1st April, 1928, to 31st March, 1929.

	£	s.	d.
L. E. Bayliss, Esq.	10	0	0
New Era Productions Ltd.	5	5	0
Oyster Merchants and Planters' Association	5	5	0
Total	£20	10	0

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Edwin Ray Lankester,

1847–1929.

Among the many notable services rendered to Zoological Science by the late Sir Edwin Ray Lankester, probably none is more enduring, certainly none stood higher in his own estimation, than the part he played in the foundation of the Marine Biological Association of the United Kingdom. For he was indeed its Founder. It is true that the conception of a Marine Laboratory, with an Aquarium attached to it, staffed and equipped for the concurrent study of Zoological Science and the practical investigation of problems bearing upon the maintenance and improvement of our sea fisheries, was borrowed, partly from Dr. Anton Dohrn's famous Zoological Station at Naples, partly from the Marine Station established by Professor McIntosh at St. Andrews and the Scottish Marine Station at Granton. It is also true that from the moment of its inception the Marine Biological Association had the cordial support of and received invaluable assistance from all the leading British Zoologists of the day, but such considerations serve only to emphasize the fact that it was due to Sir Ray Lankester's initiative that the Association was planned upon a scale that made it of national and not merely local importance, and that it was through his influence, persuasiveness, and perseverance that the funds for the building and maintenance of the Laboratory were raised. If he received generous help from others it was because he put forward his proposals in so well-thought out and concrete a form as to give assurance of success and because he was willing and competent to take upon himself the burden of overcoming difficulties which might well have deterred a less resolute character.

In retrospect it is sufficiently remarkable that so young a man—he was only thirty-six years old when the project of a Marine Biological Station was first mooted—should have commanded so much influence, not only among his scientific colleagues but among persons of all ranks and callings, as to be able to bring a scheme conceived on such generous lines to a successful issue. The truth is that this relatively young Professor had already made for himself a European reputation and was universally recognized as the only possible successor to Huxley in the leadership of Zoological Science in Great Britain. His lectures in

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University College, London, were famous and were attended by many besides those who were preparing themselves for examinations, and he was the author of many scientific memoirs of first-rate importance. He had begun young, for when, at the age of thirteen, he was required in the course of his studies to dissect an earthworm, he was so dissatisfied with the existing accounts of the anatomy of that animal that he published an account of his own observations on the subject in a treatise which, if it bears the marks of immaturity, testifies to his remarkable powers of observation and analysis of morphological fact.

The eldest son of Dr. Edwin Lankester, Coroner for Central Middlesex and Founder and Editor of the *Quarterly Journal of Microscopical Science*, Ray Lankester was brought up in scientific surroundings from his earliest years and as a boy became acquainted with many of the leading zoologists of the day. He was educated at St. Paul's School and at the age of eighteen matriculated at Downing College, Cambridge, where, among his other activities, he represented his College on the river. After two years' residence at Cambridge he entered for and was elected to a Junior Studentship at Christ Church, Oxford, and finished his scientific education in Professor Rolleston's laboratory. There he met and became a close friend of Henry Nottidge Moseley, who was destined to succeed Rolleston as Linacre Professor of Comparative Anatomy at Oxford. The two friends were inseparable ; they were placed together in the first class in the Honour School of Natural Science in 1868 ; both gained Radcliffe Travelling Fellowships and went abroad together, to Vienna in 1870 and to Leipzig in 1871. On his return from Leipzig Lankester was elected to a Fellowship and Lectureship at Exeter College, Oxford, and in 1874 he was appointed to the Professorship of Zoology and Comparative Anatomy at University College, London, a chair which he filled with great distinction, and the years in which he occupied it, 1874 to 1890, were perhaps the most active in his busy life. On the death of his friend, Professor Moseley, in 1891, he succeeded him in the Linacre Professorship of Comparative Anatomy at Oxford, but held the chair for only seven years, as in 1898 he was promoted to the Directorship of the British Museum of Natural History. He became a Knight Companion of the Bath (Civil Division) in 1907 and retired in 1908, after which year, though without an official post, he continued for a long time to exercise a guiding influence in zoological thought and did much to awaken general interest in biological problems by a series of essays entitled "Science from an Easy Chair." In 1919 he completed the fiftieth year of his editorship of the *Quarterly Journal of Microscopical Science* and received the congratulations of his many colleagues and pupils in a special number of the *Journal* dedicated to himself.

The honours bestowed upon Lankester by various Universities and

Scientific Institutions at home and abroad are too numerous to recapitulate here, but it may be recorded that he was awarded the Royal Medal of the Royal Society in 1885 and the Copley Medal in 1913, and he was President of the British Association for the advancement of Science in 1906.

This is hardly the place to survey or to attempt to write an appreciation of Lankester's numerous contributions to Zoological Science, but it will not be out of place to mention a single example as an illustration of his method of treating a zoological problem. The so-called King-Crab, *Limulus polyphemus*, is an example of a persistent type which appeared in triassic times and survives to the present day. Being an aquatic form, with respiratory organs attached to certain of its limbs, it came under the definition of a Crustacean and was classed as such by the leading authorities of the nineteenth century, although Straus-Durckheim had drawn attention to its many resemblances to Arachnida as long ago as 1829. An examination of such specimens as he had in his museum convinced Lankester that Straus-Durckheim was right, and he set out to prove it much in the same way as an eminent counsel accumulates and marshals his evidence until he leaves no loop-hole for doubt in the minds of the jury he is addressing. He obtained a consignment of Limulus from America (it is common enough on the Atlantic coast of N. America, but is not found in our seas) and submitted its anatomy to an exhaustive analysis, the results of which were published in a famous treatise entitled "Limulus an Arachnid" (*Q.J.M.S.*, Vol, XXI, 1881). Of this, and subsequent memoirs on the same subject, it has been well said that he and his pupils compared the King-Crab with the Scorpion, segment with segment, organ with organ, tissue with tissue, almost cell with cell, until he had established the connection between them beyond all possible doubt. For thoroughness, exactitude, and morphological insight this work cannot be surpassed, and we mention it here as a characteristic example of the close attention to detail and the clarity of exposition which are the hall-mark of all his scientific work. He himself regarded this essay as the best he had produced, and in the well-known portrait by Collier he is represented as lecturing on Limulus, with a specimen lying on the table and diagrams of its appendages on the blackboard.

The story of the foundation of the Marine Biological Association is told in the first number of the Journal of the Association, now out of print and difficult to obtain. A leading article in *The Times* of March 1st, 1884, announced that a meeting would be held on that day in the rooms of the Linnean Society to consider a proposal to found a Marine Station for the joint purpose of encouraging the study of marine zoology and making a scientific study of questions relating to sea fisheries. The article was written by Ray Lankester. The time was propitious, for public attention

had been attracted to our sea fisheries by the successful Fisheries Exhibition recently held in South Kensington, and the meeting was largely attended. Professor Huxley was in the chair, and among those who spoke in favour of the proposal were the Duke of Argyll, Sir Lyon Playfair, Sir John Lubbock (afterwards Lord Avebury), the Earl of Dalhousie, Professor H. N. Moseley, and Professor (afterwards Sir William) Flower. The ground had been carefully prepared; the proposals submitted to the meeting were of a kind to appeal with equal force to scientists, statesmen, and men of business, and were adopted unanimously. The Association was launched on its career with Professor Huxley as President and E. Ray Lankester as Honorary Secretary. The first step had been taken, but much remained to be done, in particular it was necessary to raise a large sum of money to build and provide for the maintenance of the projected Laboratory and aquarium. The burden of this work fell upon the Honorary Secretary, and so successful was he in his appeal to various interests that at the first Annual Meeting held in June, 1885, he was able to announce that the subscriptions amounted to £8000 and a year later this sum was increased to £15,000. After much discussion and enquiry it was resolved that the Laboratory should be built at Plymouth, the deciding factors in the choice being the generous contributions made by Messrs. John and Robert Bayly, who were deeply interested in the welfare of the fishermen of the district, and the richness of the marine fauna testified to by Mr. C. Spence-Bate, F.R.S., a resident in the city, and there was the additional advantage that the War Office offered on very favourable terms the site on which the Laboratory now stands. No time was lost in getting to work. Mr. Walter Heape was appointed Director of the Laboratory and Assistant Secretary, and Mr. J. T. Cunningham, who had been for three years Superintendent of the Scottish Marine Laboratory at Granton, was appointed Naturalist in charge of fishery investigations. In spite of great difficulties, due to lack of accommodation and equipment, work was begun almost before the commencement of the building of the Laboratory, and in spite of the unfavourable conditions a large amount of research was got through in the two years before the Laboratory was ready for occupation. After the many delays apparently inseparable from a building contract, the Laboratory was formally opened on June 30th, 1888, when the large and distinguished company present was entertained at lunch by the Prime Warden of the Fishmongers' Company who had been, and continue to be, generous patrons of the Association.

Though the Association was fairly launched on its career, the difficulties confronting it were great. So much had been spent on building that only a small sum remained for maintenance. The income amounted to less than £900 per annum, and this had to provide for the salaries of a

Director, a Naturalist, a caretaker and engineer, a fisherman and his assistant, and a Laboratory servant, in addition to the upkeep of the Laboratory and library, the hire of boats, and the publication of the Journal. The work of the naturalists was restricted for want of sea-going boats and fishing-gear. At first the only boat available for daily use was a half-decked 4-ton hook-and-line fishing-smack, to which a rowing boat and a small and not very seaworthy steam-launch were subsequently added, but none of these could venture far outside Plymouth Sound except in settled fine weather, and much time was cut to waste in beating against unfavourable winds and in the calms so frequent at Plymouth in the summer months. At times it seemed impossible to achieve the ends proposed by the Association, but Lankester was not to be deterred by difficulties and had the gift of imparting a large share of his own resolution to those who worked under him. In those early days, also, the work of the Association was largely assisted by voluntary helpers, notably by the late Professor W. F. R. Weldon and Dr. G. H. Fowler, who were inspired by Lankester's enthusiasm to take up their residence at Plymouth and to work whole-heartedly for the success of his venture.

In the difficult years following the opening of the Laboratory, Lankester was a frequent visitor to Plymouth and entered with great care and minuteness into all the details of its organisation. In those days the scientific staff spent a large part of their time at sea, sometimes in trawlers, more often in the little fishing-smack belonging to the Association ; sometimes in a tug hired for the purpose of a more distant expedition. This aspect of the work had a great attraction for Lankester and he took as full a share in it as his constitutional inability to find his sea-legs would admit. He would sail across the Sound and make long expeditions on foot for the purpose of shore collecting, but only on rare occasions, usually when Canon A. M. Norman was staying at Plymouth, would he venture outside the Breakwater. In most respects there was little in common between the Professor and the dignitary of the Church, but the latter's knowledge of the British marine fauna was unrivalled and Lankester held him in great respect on this account. The Canon was no better a sailor than the Professor, and united as they were in their love of marine zoology they were equally at one in their sufferings when the dredge was brought aboard and its contents had to be examined whilst the little vessel was pitching heavily in a lively sea.

Though there were changes in the staff of the Laboratory Lankester's unremitting exertions, backed by the goodwill of his friends, maintained the work of the Association in such a state of efficiency that when in 1899–1901 the Government was asked to co-operate in an International Investigation of the North Sea, he could claim successfully that the only organisation in England with a staff trained to undertake the particular

kind of work required was to be found in the Marine Biological Association. From that date it has received the steady support of successive Governments and its activities have increased until it has arrived at its present position, a tribute to the energy and foresight of its Founder and President for the last thirty-nine years.

It is difficult to estimate how much of the success of Lankester's undertakings, including the Marine Biological Association, was due to his pre-eminent ability as a zoologist and how much to the influence he exercised over men in all stations of life who were not primarily interested in any branch of science. It cannot be said that his influence extended over all sorts and manners of men, for it was his foible that he was called upon to detect and wage war upon imposture in whatsoever form it might present itself. On one occasion at least his exposure of a spiritualistic impostor was a subject for much merriment and won general approval. But as he was equally intolerant of pedantry and pretentiousness, and did not always discriminate sufficiently clearly between these weaknesses and imposture, he incurred a good deal of hostility by carrying his war into the camps of people who took themselves and their opinions and conventions very seriously. But his too great readiness to scent out imposture was balanced by an unerring faculty for discovering real talent, and he was cordial in his appreciation of those in whom he discerned it. By the exercise of this faculty he surrounded himself with a devoted band of pupils and colleagues to whom he was at once master and *bon camarade*. To his pupils and assistants he was indeed something of a hard master, expecting from them attainments commensurate with his own. But if exacting he was appreciative, never withholding a generous meed of praise for good work ; praise that was the more esteemed because the recipients knew well that it was bestowed only where it was deserved. If he made his assistants slave for him, he was ever mindful of their interest and exerted himself to obtain for them the promotion that he considered their due. His manner with young men was charming. Once he was assured of their worth he admitted them to terms of close though always respectful intimacy, and those who had the privilege of being included among his protégés can recall many an evening's gathering in which wit and wisdom were blended in discussions that lasted well into the small hours of the morning.

Though much of his earlier experience had been gained in Vienna and Leipzig, and he had been largely influenced in his youth by the writings of Ernst Häckel, in later years Lankester attached himself to the French school of zoologists rather than to the German. For him Paris was a more congenial city than a German university town, and he liked serious discussion to be salted with humour and gaiety. Not that he confined his appreciation to Gallic wit, for he reckoned among his most intimate

friends such kindred spirits as Professor A. A. W. Hubrecht of Utrecht and Professor Ed. van Beneden of Liége.

Born in the tenth year of Queen Victoria's long reign, Lankester must be counted among the great scientific figures of the late Victorian period. It is now the fashion, among such as think to increase their own stature by belittling the giants of a former age, to depreciate that period. But should we not rather say, in the words and the spirit of the University bidding-prayer, "let us praise great men"? For not only did they add largely to our knowledge, but they also fought for and won the freedom of scientific thought which is our inheritance.

G. C. B.

Experiments in the Sea on the Growth-Inhibitive and Preservative Value of Poisonous Paints and other Substances.

By

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With Some Chemical Analyses by the Government Chemist.

With 20 Figures in the Text.

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PART I. BIOLOGICAL INVESTIGATIONS.

INTRODUCTION.

OBSERVATIONS on breeding (**1**, 1914; **2**, **3**, 1920) and experiments on the rate of growth of marine invertebrates (**4**, 1914; **5** to **9**) have been carried out since 1911 (excepting the war period).

The particular objects of these researches were stated (**1**, 1914, p. 312) to be :—

"(1) to establish the age of common marine invertebrates.

(2) to determine the minimum age at which these forms begin to breed.

(3) to examine the rate of growth at different seasons of the year and *under different conditions.*

(4) to investigate the fecundity of different forms so far as possible.

(5) to collect the scattered literature on these subjects."

During the course of that work it was realised that the general observations being made would form an invaluable control and basis for experiments, particularly for investigating the fundamental properties and the efficacy of anti-fouling paints, i.e. paints having usually poisonous properties. These paints, as is well known, are used on the bottoms of ships to prevent marine organisms from settling and growing there. Slight growths on the bottom of a ship seriously reduce the speed of the vessel and increase the time of making a given passage in proportion to the amount of such growth, i.e. fouling. The debasement of the immense amount of capital involved in the loss of time in passage due to the fouling of vessels, and in their docking for scraping and repainting the bottom, is a sufficient indication of the great economic importance of methods for maintaining the bottoms of ships free from growths. In this pioneer research, which was begun in 1919, it was found that certain so-called anti-fouling paints had only a slight anti-fouling value (even on stationary objects), while others retained a poisoning property up to $3\frac{1}{2}$ years. Publication of the work has been delayed by unavoidable circumstances.

Object of the Research.

The object of the research was to compare growths on anti-fouling paints (A.F.P.) on experimental material composed of painted shells and painted boards and controls placed in the sea in a number of different situations, while observing normal general growth in the same and similar situations in the locality at the same time. By observing the experimental material over a period of years it was possible to determine the age at which particular paints lost their anti-fouling property, and to investigate by chemical analyses the concentration of the poisonous ingredients left in the paints when the poisonous property was lost, or near the point of being lost.

It is known that marine organisms grow more abundantly in certain localities or at certain tidal levels than in others (**10**, **11**). Therefore to test the value of anti-fouling paints in the sea it is advisable to expose these to as great a variety of conditions—to ensure as great a variety of infection from the larvæ or young of different marine organisms - as is possible, since some marine organisms (e.g. certain algæ and Tubularia) are undoubtedly less affected by anti-fouling paints than are others. Moreover, in English waters there is undoubtedly on the whole a seasonal variation in growth and reproduction (see **1** and p. 399), and it is a fact that *all growths on the bottom of floating ships begin by young or larval free-swimming forms settling on the bottom of the ship.* Thus the seasonal variation in reproduction in England and other temperate waters renders surfaces covered by anti-fouling paints liable to infection (and therefore

testing) by larvæ less in the winter period than at any other. All these considerations—in addition to the probability of infection in the infective period –are important in testing the value of an anti-fouling paint. To realise the efficacy of the poisonous paints and other substances the reader is directed especially to the records of normal growth given in **1**, 1914 ; and pp. 396–399, 416, 420, and 424 herein.

The Substances Tested Experimentally.

The following paints and other materials were tested in one or more experiments : numbers I to VI and number XI being proprietary compositions the same as, or similar to, those placed on the market ; No. IX, ship-chandlers' black varnish, being coal tar diluted to the required thinness by naphtha :—

LIST (I) OF THE SUBSTANCES TESTED EXPERIMENTALLY.

No. of Paint or other substance.	Designation.	Colour.	Property.*
I	Anti-fouling composition	Reddish brown	A–F
II	,, ,,	Dark green	A–F
III	Anti-corrosive only, composition	Black	A–C
IV	Anti-fouling composition	Reddish brown	A–F
V	Anti-corrosive only	Black-bronze	A–C
VI	Anti-fouling composition	Red	A–C & A–F
VII	Clean surface (Control)	White or greyish white	
VIII	Red oxide of iron	Red	
IX	Black varnish	Black	
X	Tar	Black	
XI	Anti-fouling composition	Light green	A–F
XII	Aluminium paint	Silvery	
XIII	Copper sheets	Reddish brown	
XIV	Zinc sheets	Metallic grey	
XV	A Grey paint	Grey (opaque)	

Disposal of the Experimental Material in the Sea.

In order to expose the anti-fouling paints and other substances to different conditions in the sea, experiments were carried out in three situations in Plymouth Sound, namely :—

(1) on an experimental raft submerged in Cawsand Bay.

(2) on the piles of the West Wharf, Great Western Railway, in Millbay Docks, Plymouth, at the level of low-water spring tides.

(3) on the piles of the Promenade Pier, at the level of low-water spring tides.

* A–F signifies anti-fouling ; A–C anti-corrosive.

In these three situations the general conditions are somewhat different.

(1) In Cawsand Bay the water is relatively clean, clear, and usually of high salinity, but the tidal current is slight. In this situation the experimental material was constantly immersed on a wooden raft ($20\times5\times2$ feet) at a depth of 1 to 2 feet below the surface. One of the experiments was carried out in direct exposure to light, but the three others were in shade or subdued light. Wave-action is strong only with easterly winds, but the experimental material would be almost continuously in motion due to the roll and pitch and up-and-down movement of the raft.

(2) At the Great Western Railway Wharf the water conditions are more foul than at the Promenade Pier, for besides pollution from the adjacent city sewer, fouling occurs from (*a*) occasional discharges of foul water from the inner dry dock, (*b*) occasional discharges of warm and foul water from vessels unloading alongside the wharf, and (*c*) the loss of grain and china clay from vessels loading and unloading alongside. Tidal currents are negligible in this situation ; at dead low-water spring tides the experimental material would be exposed only to diffuse daylight. The salinity in this locality is estimated as being not very different from that prevailing at the Promenade Pier (**2, 29**).

(3) At the Promenade Pier the water must be regarded as mostly heavily charged with bacteria derived from the adjacent sewer outfall, but relatively pure on the latter part of the flood of spring tides. The salinity is variable and of a lower mean than in Cawsand Bay, but, as in Cawsand Bay, the tidal current is slight. The material was mostly in a subdued light (under water under the Pier), but would be exposed to air, wind, and daylight (but not to direct sunlight) at the middle of the day (**11,** p. 280) at spring tides which were slightly lower than the average. Wave-action is fairly strong with south to east winds.

Description of the Experimental Material.

The anti-fouling properties of the paint compositions and the materials were tested by painting them on scallop shells (*Pecten maximus*) and on test-pieces of wood (Elm and Deal). The painted shells were previously bored with holes of a distinctive size or position, and either strung with tarred or clean yacht manilla around piles in the sea and inside or underneath the raft. Other shells were nailed on the bottom of the Cawsand Bay raft ; test pieces of wood were nailed on to old Jarra wood piles at the Great Western Railway Wharf (G.W.W.), and some were tied with tarred rope to cement piles in the same wharf.

Two good coats of paint composition (or other material) were given to all shells and test-pieces of wood, i.e. battens. In all cases the application

was made as thoroughly as it can be by brushing the paints well in on to dry surfaces and with rare exceptions *the painted surfaces were well dried before being immersed in the sea.* Thirty shells and five wooden test-pieces were used to test each proprietary anti-fouling paint and other substance at Cawsand Bay; and ten shells and one batten to test each of them at the Great Western Wharf, Millbay Docks. One anti-fouling paint was tested by sixteen shells—as were several other materials—at the Promenade Pier, but complete details of the tests are best given with each experiment. In all experiments with shells a number of clean shells equal to or greater than the number of the painted shells was put out with the latter as a control experiment; untreated test-boards were also used as controls alongside treated battens.

List (II) of Experiments.

The following list of the experiments carried out will be useful for reference :—

Series I.—Cawsand Bay. Experiments on and in a submerged but floating raft* (see Figs. 19 and 20, pp. 426 and 427) put out in the sea on July 16th, 1919, and moored in 3 fathoms of water about 150 yards N.W. by N. from the end of the pier at Pier Cove (Pier Cellars). The raft was stoutly made of a wooden frame 20 feet by 5 feet by 2 feet deep, on which were nailed 4 by 1-inch battens of wood on the bottom and sides, so as to leave about 1 inch of space between adjacent battens. It was divided into three compartments, over which lids—having the same structure as the bottom and sides—were fitted. Mooring was effected by a central swivelled attachment at the bottom of the raft, and sufficient slack mooring chain was allowed to permit of the raft being turned over completely.

Experiment. Designation of experiment.	Duration.	No. of times visited.	Situation on raft.
A. Wooden ladder	Aug. 18th, 1919–Oct. 9th, 1920	9	on bottom and outside
B. Board of squares	,,	9	,,
C. Foot battens exposed to light	,,	9	at sides and outside
D. Shells under raft (1) fixed (2) enstrung	Aug. 18th, 1919–Oct. 23rd, 1920	9	at bottom and outside
E. Shells inside raft (1) fixed (2) enstrung	,,	9	inside

* This raft was originally designed by Dr. E. J. Allen for acclimatising marine animals (to low pressures) prior to transferring them from the sea to the Plymouth Aquarium tanks. By a modification of the structural parts by the writer, similar smaller rafts were designed for the study of the bionomics of Teredo by Potts (**12**, 1923) and the Institute of Civil Engineers (**13**, 1924).

Series II.—West Wharf, Millbay Docks, Plymouth. Shells were strung on tarred rope and secured around cement piles at low-water spring tide level. Boards were nailed to old Jarra piles at about low-water spring tide level.

Experiment.	Duration.	No. of inspections.	Situation.
F. Three-feet boards (red pine)	Aug. 27th–28th, 1919–March 7th, 1923	15	L.W. spr.
G. Shells on rope	Aug. 28th, 1919–April 23, 1921	8	,,

Series III.—Promenade Pier, Plymouth. Shells and sheets of copper and zinc were strung on tarred and clean rope around the inner piles under the Pier at low-water spring tide level.

Experiment.	Duration.	No. of inspections.	Situation.
H. Shells and metal sheets on rope	June 18th, 1919–Feb. 21st, 1920	8	L.W. spr.
J. Raft, Cawsand Bay	March–Oct., 1912	–	within the battens
K. Bathing rafts, Plymouth Sound	April–Oct., 1912–28	–	on lower surface

LIST (III) OF THE CHIEF* ORGANISMS GROWING ON OR IN THE EXPERIMENTAL MATERIAL AND CONTROLS.

PROTOZOA.

Folliculina ampulla, **20**, p. 257

PORIFERA.

Sycon coronatum, 185
Leucandra fistulosa
Leucosolenia sp., *185*
Halichondria panicea, 186
Halichondria sp.
Hymeniacidon sanguineum, 186

CŒLENTERATA.

TUBULARIA LARYNX, 190
Plumularia pinnata, 199
OBELIA GENICULATA, 193
Bougainvillea ramosa, 189
Clytia Johnstoni, 193
Gonothyræa Loveni, 194
Actinoloba dianthus, 205
(=*Metridium senile*)
Sagartia viduata Gosse, **18**, p. 111
(=*S. anguicoma* [Price])

POLYCHÆTA.

POMATOCEROS TRIQUETER, 232
HYDROIDES NORVEGICA, 232
Serpula vermicularis, 232
Sabella pavonina, 231
Polydora ciliata, 227
Sabella sp., small unidentified

POLYZOA.

Umbonula verrucosa, 262
BUGULA FLABELLATA, 260
Membranipora sp., *260*
CELLULARIA sp., prob. *neritina*

ECHINODERMATA.

Antedon rosacea, 207
Echinus miliaris, 210

MOLLUSCA.

Tergipes despectus, 279
Galvina exigua, 279
Galvina picta, 279

* The names given in capitals are the predominant organisms in each group causing the fouling of the ships' bottoms and buoys. The figures in italics refer to pages in reference **10**.

Facelina Drummondi, 280
Dendronotus frondosus, 282
Teredo norvegicus
Pecten operularis, 287
Anomia aculeata
Mytilus edulis, 286
Helcion pellucida, 268
Patella vulgata, 268
Concholepas peruviana

Crustacea.

Balanus sp., probably *crenatus, 237*
B. perforatus, 237
B. tintinnabulum, **19**, p. 212
Limnoria lignorium, 243
Chelura terebrans, 241
Jassa sp., probably *falcata, 241*
Conchoderma virgatum, **19**, 144
C. auritum, **19**, p. 144
Lepas Hilli, **19**, p. 110
L. anatifera, **19**, 108
Nautilograpsus minutus (=*Planes*), **22**, p. 135
Pilumnoides perlatus, **23**, p. 544, Plate 50
Cancer pagurus juv., *256*
Porcellana longicornis, 254
Carcinus mœnas, 257
Leander serratus, 249

Tunicata.

Diplosoma gelatinosum, **27**, p. 87 (=*Leptoclinum* Hartmeyer, **28**, p. 1455)
Botryllus violaceus, 298
Botrylloides rubrum, 298
Morchellium argus, 297
Ascidiella aspersa, 296
Ciona intestinalis, 296
Molgula ampulloides

Algæ.*

Laminaria saccharina
L. digitata
Ulva latissima
Enteromorpha intestinalis

Detailed Account of the Course of the Experiments.

series I. cawsand bay raft.

Experiment A. Wooden ladder experiment.

In this experiment a ladder was made 3 feet long with eight rungs and fixed across the bottom of the raft. The side pieces of this ladder consisted of two battens of elm, 3 feet by 4 inches by 1 inch, while the rungs were made of smaller battens of elm, 1 foot by 2 inches by 1 inch. Six of the rungs were painted with the proprietary paints I to VI, noted on page

Fig. 1.—Showing the arrangement of the test-pieces treated with substances I to VI and VIII in the ladder experiment (A) on the Cawsand Bay Raft, begun August 18th, 1919 (reduced ca. $\frac{2}{17}$).

Each rung of the ladder was painted with the substance designated by the number (see p. 376) as well as the rectangular areas opposite the end of each rung. No. VII was left untreated as a control.

Fig. 2.—Same as Fig. 1, and showing the distribution of the growths of *Tubularia larynx* found on the test-pieces on September 30th, 1919, after 6 weeks' exposure in the sea.

I, II, and IV are clean and VI has a little growth; all the other test-pieces have acquired heavy growth.

Fig. 3.—Same as Fig. 1, and showing the distribution of various growths on October 9th, 1920, after about 14 months' exposure in the sea.

The growths shown are chiefly Ciona and Diplosoma with some Pomatoceros, Anomia, and colonies of hydroids.
I, II, and IV are still almost clean, but all the other test-pieces have a luxuriant growth.
Figs. 2 and 3 are reproduced from field sketches and notes. The taking of photographs at a later stage (as intended) was prevented by loss of the raft in a gale.

* Many unidentified, including a brown filamentous Alga and a Polysiphonia sp.

FIG. 1 AUG. 18 1919

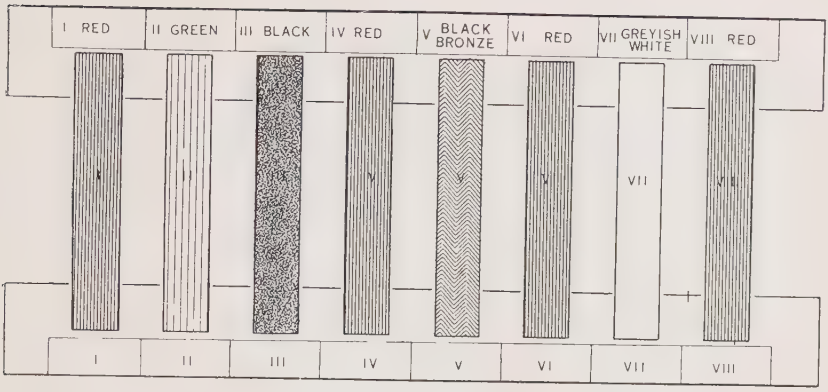


FIG. 2 SEPT 30 1919

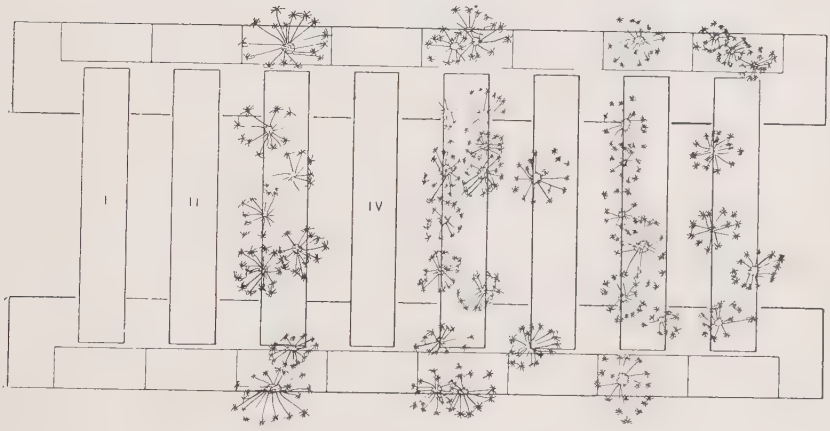
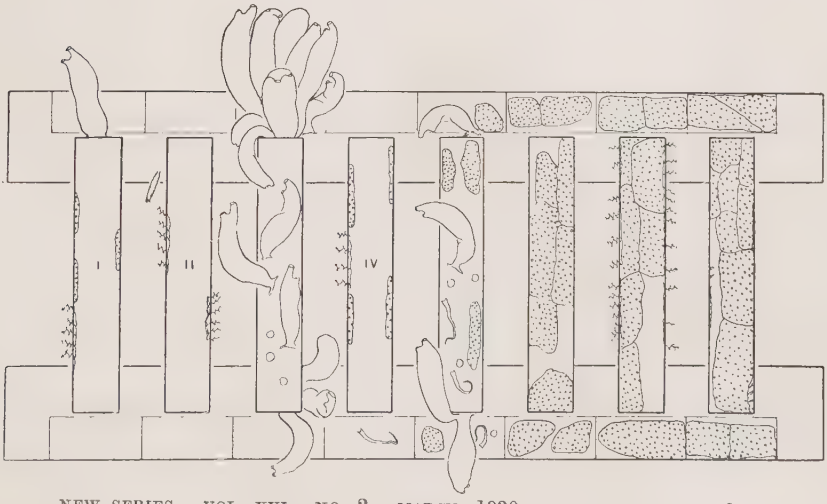


FIG. 3 OCT. 9 1920



376, one (VII) was left clean, and the remaining one (VIII) painted with red oxide (of iron) paint. An area on each of the outer sides of the ladder opposite the rungs was painted with the same material as the adjacent rung, as is shown in Fig. 1, p. 381. In addition the inner sides of the ladder were painted respectively with coal-tar between rungs 2 and 3 and with black varnish between rungs 5 and 6 (see Fig. 1). The remaining part of the sides of the ladder was left clean.

The ladder was fixed to the raft and immersed in the sea on August 18th, 1919. On September 30th, 1919, six weeks later, it was examined, with the result shown in Fig. 2, page 381, and when examined on the last occasion, on October 9th, 1920, it showed the growths depicted in Fig. 3, page 381. This experiment was not reported on again after October 9th, 1920, and the experiment, and indeed all the experiments on the raft, were lost after a gale on December 25th–26th, 1920.

In Table I below are given reports on the growths found on the two visits recorded and the condition of the paints on October 9th, 1920.

Table I.

Reports on Ladder Experiment (a).

Designation and colour of surface.	Growths found on Sept. 30th, 1919 (exposed 6 weeks).	Growths found on Oct. 9th, 1920 (exposed *c.* 14 months).	Condition of paint on Oct. 9th, 1920.
I Reddish brown A–F	None	A little Diplosoma, a few small hydroid colonies, and a little Podoceros	Nearly all gone
II Green, A–F	None .	Practically clean : only a few small colonies of hydroids	Very soft
III Black A–C	Large growth of Tubularia and some small Pomatoceros	Enormous Ciona and some Anomia	Apparently good
IV Reddish brown A–F	None	A little Diplosoma and hydroids and one large Pomatoceros	Fairly good
V Blackish bronze A–C	Large growth of Tubularia and some small Pomatoceros	Large Ciona, some Anomia, Pomatoceros, Diplosoma and hydroids	Apparently good
VI Reddish brown A–F	Slight growth of colonies of Tubularia	Covered with Diplosoma which also extends in parts over the paint	Mostly washed off
VII Greyish white untreated	Large growth of Tubularia and some small Pomatoceros rather less than in III and V	Covered with Diplosoma and hydroids	Originally clean
VIII Red, A–C	Same as on VII	Covered with Diplosoma	Mostly washed off

Results of Experiment A.

In this situation and under the conditions described the poisonous paints I, II, and IV retained their growth-inhibiting properties during about fourteen months and only permitted slight growth on parts where the paint had probably washed off more rapidly than in others. The anti-corrosive paints III and V, as well as the clean board VII and the red oxide board VIII, all developed extensive or very extensive growth, within as short a period as six weeks, and developed heavy growths subsequently. The anti-fouling paint VI also developed a slight growth in six weeks and a heavy covering of growth later, and is therefore inefficient as an anti-fouling paint under these conditions. At the end of the experiment, however, paints III and V were in a better condition than any of the others. It is of interest to note that the red oxide was mostly washed away in just over a year. The anti-fouling paints II, IV, and I were efficient in this order after about fourteen months in the sea under these conditions.

Experiment B. Board of Squares.

In this experiment a single piece of wood, 3 feet by 4 inches by 1 inch, was prepared by painting 4 inch squares with each of the paints I to VI and VIII, and leaving one square (VII) and a strip of 2 inches at each end clean (see Fig. 4, p. 385). This board was screwed on the bottom of the Cawsand Bay raft in the same way as in the ladder experiment (p. 380) and at a little distance from it. The board was screwed to the bottom of the raft and exposed to the sea on August 18th, 1919; it was examined on September 30th, 1919, after being in the sea six weeks, and last seen on October 9th, 1920. On September 30th, 1919, the growth found on the board is shown in Fig. 5, p. 385, and is described as follows :—

Table II. Report on Board of Squares Experiment, September 30th, 1919.

	Designation and colour of surface.		Growths found on Sept. 30th, 1919 (exposed 6 weeks).
I	Reddish brown ;	A–F	None.
II	Green ;	A–F	None.
III	Black ;	A–C	Three colonies of Tubularia.
IV	Reddish brown ;	A–F	None.
V	Black bronze ;	A–C	Three colonies of Tubularia ; some Obelia *with Nudibranchs and spawn.*
VI	Reddish brown ;	A–F	None.
VII	Greyish white ;	untreated	One colony of Tubularia and some small Pomatoceros.
VIII	Red ;	A–C	Also one colony of Tubularia and some small Pomatoceros.
Ends	Greyish white ;	untreated	One colony of Tubularia on one end.

On October 9th, 1920, this board was seen for the last time, and found at that time to have similar growths on each paint or surface as was shown on the rungs of the ladder experiment (see Table I, p. 382). No special report on this board was written down on this day at the moment of observation owing to the advent of bad weather conditions.

Results of Experiment B.

The results from Experiment B were in all respects similar to those obtained from Experiment A (see p. 383).

Experiment C.

On boards 1 foot by 2 inches by 1 inch, treated in the same way as the rungs in the ladder experiment (see p. 380) and exposed to light.

These boards were placed vertically on the outside at the ends of the sides of the raft with the bottom end of each board flush with the bottom of the raft. The boards were thus placed 1 to 2 feet below the surface of the water and were exposed to direct water-filtered sunlight, and possibly at times for an instant to direct light.

As in the case of experiments A and B, this experiment was begun on August 18th, 1919, examined on September 30th, 1919, and last seen on October 9th, 1920. The reports given in Table III show the varying degrees to which growth was inhibited in this habitat.

Results of Experiment C.

After six weeks in the sea the same four substances, namely I, II, IV (and VI), resisted growths of seaweed as they did of animals in the contemporaneous experiments A and B (see pp. 383–4). In the same period, i.e. August 18th to September 30th, 1919, the remaining boards III, V, VII, and VIII all became covered with a growth of seaweed, probably mainly of Enteromorpha. Contrary to experiments A and B, however, slight growths of other seaweeds manifested themselves on the former (and poisonous) compositions already on March 2nd, 1920, only seven months after immersion. After about fourteen months in the water the compositions II, IV, and I had definite growths of a short filamentous brown Alga, in contrast with the slight growths on these compositions in situations exposed only or mainly to animal growth, i.e. under the raft, while the remaining boards after fourteen months all had Laminaria as well as other growths. The paint compositions II and IV were the only ones not permitting growth of Laminaria, and there can be little doubt that they were exposed to the same or a similar degree of "infection" as the others.

FIG. 4

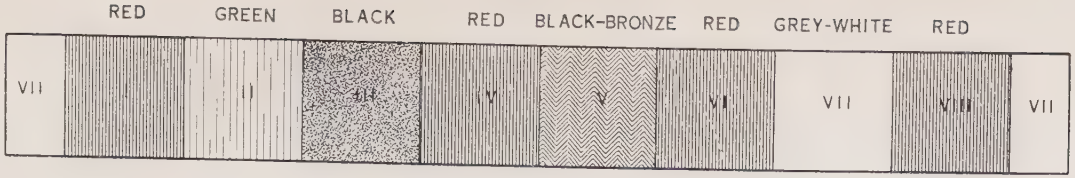


FIG. 5

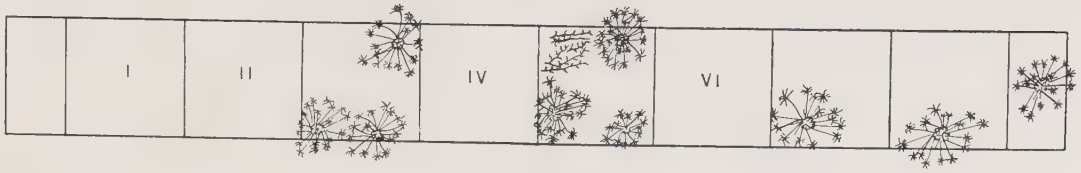


FIG. 6

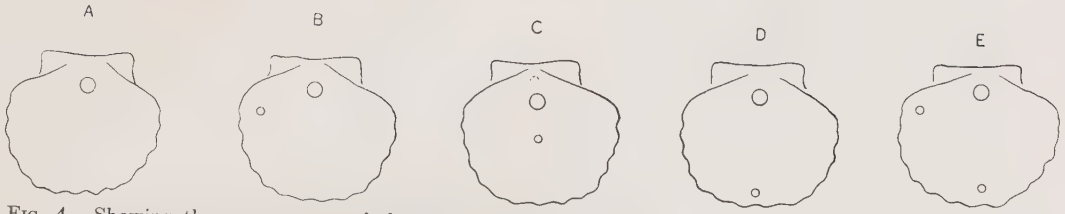


FIG. 4.—Showing the arrangement of the areas painted with substances I to VI and VIII in the Board of Squares experiment (B) begun August 18th, 1919, on the Cawsand Bay Raft.

FIG. 5.—Same as Fig. 4, showing the distribution of colonies of Tubularia on the Board of Squares experiment (B) on September 30th, 1919, after 6 weeks' exposure in the sea.

I, II, IV, and VI are clean, while all the other test-areas have acquired and permitted luxuriant growths of Tubularia.

FIG. 6.—Scheme of the borings made in the painted scallop shells to serve for their identification while exposed in the sea.

A. One sub-central hole
B. ,, and a lateral hole.
C. ,, and a central or umbonal hole.
D. ,, and a ventral hole.
E. ,, and a lateral and a ventral hole.

III Black; I Red; II Dark green; III Aluminium.
IX Black; IV Red; XI Light Green.
VIII Red.
V Black-bronze; VI Red.
X Black

Table III.

Reports on Growths on Test-pieces Exposed to Light on the Cawsand Bay Raft.

Designation and colour of surface	Growth on Sept. 30th, 1919 (exposed 6 weeks).	Growth on March 2nd, 1920 (exposed 7 mths.).	Growth* on Oct. 9th, 1920 (exposed *c.* 14 mths.).
I Reddish brown A–F	None	All with some growth of weed.	Small Laminaria and scum of a brown Alga
II Green A–F	None		Scum of brown Alga only
III Black A–C	Large growth of seaweeds (probably mainly Enteromorpha)		Small Laminaria, Balanus and a scum of brown Alga
IV Reddish brown A–F	None	The Green board appears† to have relatively little growth on it.	Scum of brown Alga only
V Black-bronze	Large growth of seaweed (probably mainly Enteromorpha)		Small Laminaria, small Ulva, good colony of red weed and Anomia
VI Reddish brown A–F	None		Laminaria of medium size, Enteromorpha and Ulva
VII Greyish white untreated	Covered with a growth of weed (probably mainly Enteromorpha)		Laminaria of medium size, Enteromorpha and Ulva
VIII Red A–C	Covered with a growth of weed (probably mainly Enteromorpha)		do.

The boards were fixed on one side of the raft in groups of four near each end in the following order and relation to the ends of the raft : —

(*a*) One end, IV, III, I, II—middle—V, VIII, VI, VII, the other end (*b*).

At the (*a*) end I and III grew Laminaria, as well as those at the (*b*) end, and Laminaria was growing over most of the lower sides of the raft. On the other hand, all the boards at the end (*a*) had a brown scum and no green weeds (Enteromorpha and Ulva), while the boards at the (*b*) end all grew green weeds ; the examination of these four boards had to be performed rapidly, and it is not now certain that these boards had not also a growth of the brown algal scum.

* All the painted boards had more or less paint remaining, but a careful examination could not be made on this date owing to the onset of bad weather.

† There was too much wind and wash of the waves to examine the boards thoroughly on this visit.

Thus, although it is unlikely, it is possible that the general conditions were not favourable for the settling and growth of the green weeds at the (*a*) end of the raft. There was a good general growth of the green weeds on the top and sides of the raft, but the detailed distribution was not recorded at the time, and in future experiments it is clear that

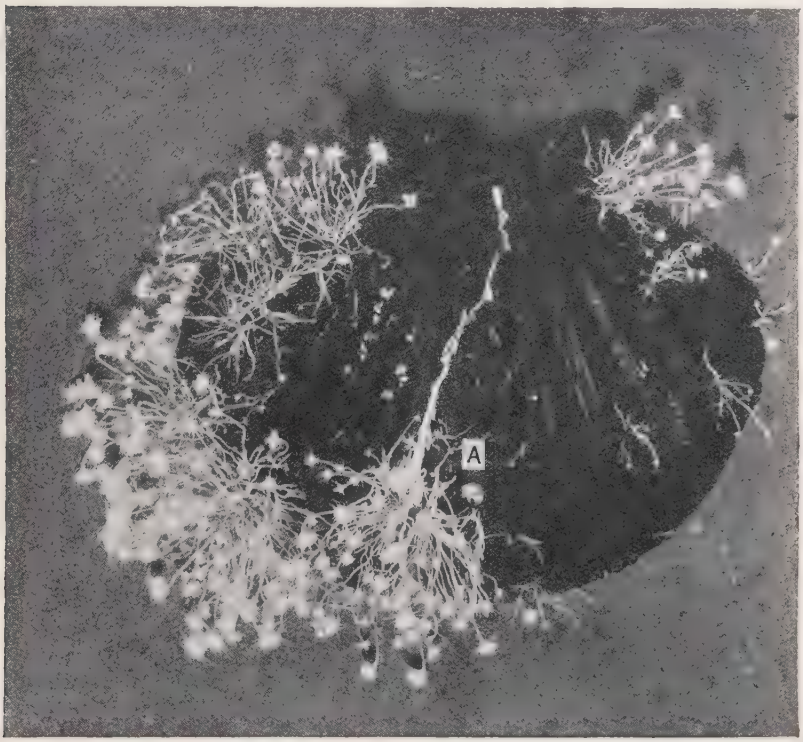


FIG. 7.—Photo of shell with a heavy growth of *Tubularia larynx* from Experiment D, Cawsand Bay raft, coated with substance No. V; exposed in the sea from August 18th, 1919, to September 30th, 1919. (Photo by D. P. Wilson.)

The distinguishing mark of the shell, a small hole ventral, is shown below A, near the lower margin of the shell to the right of the white vertical line in the middle of the shell. The shell was broken into two parts to permit the preservation of the Tubularia in a bottle. A large colony of this hydroid has been taken from the shell in order to expose the distinguishing hole.

periodical observations of this kind should be made. Under the conditions of the experiments A, B, and C there are distinct indications that the better toxic paints II, IV, and I are less toxic to marine algæ than to marine animals, but in order to confirm this indication it will be necessary to know whether light itself affects the toxicity of the paints.

In this respect a chemical analysis of painted surfaces exposed contemporaneously in strongly lighted and diffusely lighted, but otherwise equivalent, situations respectively would probably yield significant information.

Experiment D.

Shells of the scallop, Pecten maximus, *were painted with a variety of substances, strung on tarred rope, and secured to the bottom of the outside of the raft in Cawsand Bay.*

Each of the substances (I to VI and VIII, see p. 376) being tested was painted on to a variable number, about ten, scallop shells, which

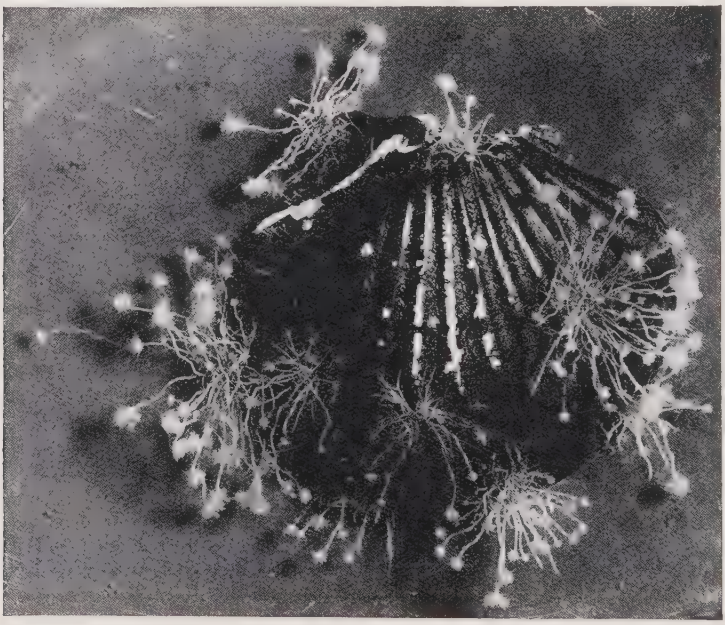


FIG. 8.—Photo of scallop shell from Experiment D_1, Cawsand Bay raft, painted with No. III substance (Black) showing the growth of *Tubularia larynx* on September 30th, 1919, after 6 weeks' exposure in the sea. ($\times$ ca. $\frac{3}{5}$.) (Photo by D. P. Wilson.)

Compare Fig. 2, p. 381, and Fig. 5, p. 385. The shell was broken at one corner of the hinge to permit entry into a bottle for preservation. The shell is viewed from the rough outer surface and now shows signs of rubbing on the radiating ridges

were marked by a boring in a particular place for identification in the manner shown in Fig. 6, p. 385. The painted shells with clean control shells were put out on August 18th, 1919, and examined on September 30th, 1919, October 9th, 1920, and brought in and preserved October 23rd, 1920.

The following note was written at the time the shells were put out, and as it is of importance in interpreting the results obtained it is given as written :—

"Two good coats of the paints were given to each shell. Unfortunately, some shells of all paints showed signs of rubbing on the smooth surface when the shells were put out. This was due to the necessity of carrying the shells to the wharf in baskets, during which time the jolting rubbed small patches of paint off the smooth surface of the shells. No case was seen of the paint on the rougher surface being broken. It is, therefore, obvious that paints of this kind chip or rub off very readily on a smooth surface, a fact of importance to be remembered in working with it, and drawing deductions from experiments. On recording subsequent growth on these shells, it is therefore necessary to take into account the condition of the paint at the time an observation is made. These rubbed shells may give valuable information regarding the arrest (or otherwise) of growths by paint if the rubbed areas permit growth and the paint composition inhibits such."

It will be shown later that marine growths were frequently observed on areas of shells denuded of paint, and confined to such areas by the inhibiting (i.e. poisoning) action of the adjacent painted area. Moreover, a painted shell might give an erroneous indication of permitting growth if denuded areas occur and fail to be observed ; and indeed in all experiments of this kind such a possibility must be constantly borne in mind.

The growth observed on these shells is shown in Table IV below and in Table V, p. 390, and Figs. 7, p. 387, and 8, p. 388.

It is noteworthy that *some* of the suspended shells in this experiment grew Laminaria, and were doubtless exposed to dim light.

Table IV. Experiment D_1.

Reports on Growths on Treated Shells suspended outside the bottom of the Raft in Cawsand Bay on August 18th, 1919.

Designation and colour of surface.	Growth observed on Sept. 30th, 1919 (exposed 6 weeks).	Growth observed on Oct. 9th, 1920 (exposed *c.* 14 months).
I. Reddish brown, A–F	None, except small Tubularia at edges of one shell	
II. Green, A–F	None	All shells except No. II, green, with more or less growth similar to that on the boards in Experiment A (see Table I, Oct. 9th, 1920, p. 382)
III. Black, A–C	Large growth of Tubularia and some Pomatoceros	
IV. Reddish brown, A–F	None	
V. Black-bronze, A–C	Not observed. See Table VI, p. 392	
VI. Reddish brown, A–F	None, except a little Tubularia on edge of one shell	
VII. Greyish white untreated	Large growth of Tubularia on shells at one end of raft, very little growth at the other end	
VIII. Red, A–C	Fair growth of Tubularia	

Table V. Experiment D_1.

Report on Growths and condition of the Paint on Treated Shells suspended outside the bottom of the Cawsand Bay Raft on October 23rd, 1920, when the Shells were brought to the Laboratory and Examined and Preserved. (See Fig. 9, p. 393 and Fig. 10, p. 395.)

Designation and colour of the surface and the number of shells.	Condition of the paint on the (a) smooth and (b) rough outside surface of the shells.	Growth on the shells on (a) smooth (inside) and (b) rough (outside) surface.
I Reddish brown A–F 7 shells.	(a) *Smooth inside surface.* Almost all washed off.	(a) Almost all covered with Tubularia and other hydroids. Some Balanus, Pomatoceros, Anomia, much Diplosoma, Ciona (9·5 cm. contracted).
	(b) *Rough outside surface.* Almost all washed off except in the hollows.	(b) Organisms overgrowing paint in parts, but restricted in some, but not in others, by the paint. Some Balanus, Pomatoceros, many Anomia, much Diplosoma and extensive growth of Tubularia and other hydroids.
II Green A–F 6 shells.	(a) *Smooth inside surface.* Nearly all washed off in all but one, which is still half-covered with paint.	(a) Practically no growth on the paint. Diplosoma and Pomatoceros are overgrowing the paint a little in parts, but on the whole the growth of Diplosoma is obviously still limited to the area of clean (i.e. denuded) shell, and shows little inclination to extend over the paint. Some Balanus, Anomia, Umbonula, Mytilus, as well as Diplosoma and Pomatoceros on the clean parts, and also Tubularia and other hydroids.
	(b) *Rough outside surface.* The paint is about half washed off on the crests, but entire in the hollows on all shells but one, which is still covered by paint.	(b) Growth nil.
III Black A–C 8 shells	(a) *Smooth inside surface.* Washing off all more or less.	(a) Covered with an abundant growth. Some Ciona up to 12 cm. (con.), some Ascidiella up to 7·5 cm. (con.). Actinoloba (greeny brown) 6 cm. at base (con.) with column 3 cm. high (con.). Some Anomia, Pomatoceros, Hydroides, Serpula, Diplosoma, Umbonula, Tubularia and other hydroids, many small Sycon on Ascidiella, large Balanus and many small tubicolous Sabellid worms.
	(b) *Rough outside surface.* None of the paint washed off.	(b) Growths entirely covered 3 shells and almost covered the remaining 5. Some Anomia, Pomatoceros, Hydroides, Umbonula, Diplosoma, many colonies of hydroids and also the seaweed Laminaria, and a red seaweed.

Designation and colour of the surface and the number of shells.	Condition of the paint on the (a) smooth and (b) rough outside surface of the shells.	Growth on the shells on (a) smooth (inside) and (b) rough (outside) surface.
IV Reddish brown A–F 6 shells	(a) *Smooth inside surface.* More than half the paint is washed off 5 shells; one with five-sixths of the paint still adhering.	(a) Some shells are covered with growth even where the paint has remained: in others Diplosoma shows restriction by the paint. Much Diplosoma and Tubularia, 1 Anomia, 2 Hydroides, 2 Balanus and 2 Mytilus.
	(b) *Rough outside surface.* The paint is almost entire on 5 shells.	(b) Three shells (one covered still with paint) have no growth. Tubularia only is present on one shell. Diplosoma is overgrowing half to one-third of the two other shells, which have also 2 Balanus and one Sabellid polychæte.
V Black-bronze A–C 5 shells	(a) *Smooth inside surface.* A very little washed off some, more than half off others.	(a) Mostly well-covered with growth of Serpula, Pomatoceros, Hydroides, Tubularia, and other hydroids, Anomia, Balanus, Membranipora, Diplosoma, and Bicellaria.
	(b) *Rough outside surface.* Three shells with paint entire but washed off one, and probably rubbing off another.	(b) The same as in (a) above with, in addition, Ascidiella and Umbonula.
VI Reddish brown A–F 7 shells	(a) *Smooth inside surface.* Almost all washed off.	(a) Covered with growth: comprising:—Many Pomatoceros, some Hydroides, Anomia, Balanus, Ascidiella 7 cm. (con.), Sabella (10·8-cm. tube), much Diplosoma, Tubularia, and other hydroids, Membranipora, small tubicolous Polychætes, *Laminaria saccharina* with roots growing around the edge.
	(b) *Rough outside surface.* A fair amount of paint left on some, but little on other shells.	(b) All shells practically covered with growth, which is obvious even over the paint. About 20 plants of *Laminaria saccharina* on one shell, and 3 other shells with 1 to 5 plants: fronds up to 96 cm. long by 15 cm. wide. Many Hydroides, few Pomatoceros, Balanus, and Anomia, much Tubularia and other hydroids, and Diplosoma overgrowing many shells. Mytilus up to 22 mm. in length.
VII Greyish white untreated 6 shells	(a) *Smooth inside surface.* Untreated.	(a) Covered with growth. Ascidiella up to 7 cm. (con.); Ciona up to 6·5 cm. (con.). Tubularia and other hydroids, many Anomia, Balanus 2 species, Umbonula, Pomatoceros, Sabella, and other tubicolous Polychætes, young Actinoloba (?), and seedlings of Laminaria.
	(b) *Rough outside surface.* Untreated.	(b) Covered with growth. Ascidiella up to 6·3 cm. (con.), Balanus, Anomia, Pomatoceros, Tubularia, and other hydroids, Actinoloba 3 × 4·5 cm. at base and column 1 to 1·5 cm. high (con.), 12 small seedlings of Laminaria.

Designation and colour of the surface and the number of shells.	Condition of the paint on the (a) smooth and (b) rough outside surface of the shells.	Growth on the shells on (a) smooth (inside) and (b) rough (outside) surface.
VIII Red A–C 5 shells	(a) *Smooth inside surface.* Almost all washed off.	(a) All covered with growth: 4 Ciona up to 11 cm. long (con.); 3 Ascidiella up to 8 cm., many Anomia, several Pomatoceros, much Tubularia, and other hydroid growth, 3 Balanus and one tubicolous Polychæte.
	(b) *Rough outside surface.* Almost all washed off.	(b) All covered with growth: *Laminaria saccharina* frond 105 cm. slightly broken × 14 cm. wide. *Laminaria Digitata* (?) 60 cm. broken × 13 cm. wide. Many Balanus, Anomia, Hydroides, some Pomatoceros, Serpula, and many colonies of Tubularia with other hydroids. (See Fig. 11, p. 397.)

Experiment D_2.

Shells of the scallop, Pecten maximus, *were painted with a variety of substances and fixed to the outside of the bottom of the raft in Cawsand Bay on August* 18*th,* 1919.

In addition to substances I to VI and VIII, black varnish, No. IX substance, p. 376, was also painted on to five shells in this experiment. These shells permitted growth in the same way as those strung under the raft (see Table V), except that the Nudibranch, *Facelina drummondi*, crawled on to and deposited spawn on the colonies of *Tubularia larynx* which were growing on some of the painted substances (as is shown in Table VI below) on September 30, 1919.

Table VI.

Report on Growth and Conditions of Paint on Shells nailed to the outside of the bottom of the Cawsand Bay Raft.

	Growth Sept. 30th, 1919* (exposed 6 weeks).	Growth Oct. 9th, 1920 (exposed *c.* 14 mths.).
I. Reddish brown A–F	None	All shells except No. II with more or less growth similar to that on the boards on Oct. 9th, 1920, in Experiment A. (See Table I, p. 382.) No. II has no growth on 5 shells. No. IV has only slight growth. No. IX has large Ciona.
II. Green, A–F	None	
III. Black, A–C	Large colonies of Tubularia and Pomatoceros	
IV. Reddish brown A–F	None	
V. Black-bronze, A–C	Large colonies of Tubularia with Nudibranch spawn and two shells with Pomatoceros	
VI. Reddish brown A–F	None	
VII. Greyish white untreated	Large colonies of Tubularia with Nudibranch spawn and Pomatoceros	
VIII. Red, A–C	Large colonies of Tubularia and Nudibranch spawn	

* Tubularia observed growing on the heads of the iron nails used for the experiment.

FIG. 9.—Photo of shells from Experiment D_1, Cawsand Bay Raft, October 9th, 1920; exposed to the sea on August 18th, 1919. See Table V, p. 390. (× ca. $\frac{2}{5}$.) (Photo by D. P. Wilson.)

I Red: with much Diplosoma and also Balanus and Hydroides, Anomia and a little Tubularia. Very little paint is left on this, the smoother, surface of the shell.

II Dark green: with Diplosoma and Hydroides growing on the hinge-line, but no growth elsewhere. The paint is shown to be washing off badly: smooth surface view of shell.

III Black: with Ciona and Diplosoma mainly, but also with Hydroides, Anomia, and Tubularia: smooth surface view of shell.

IV Red: with Diplosoma mainly and mostly confined to areas denuded of paint. The paint is washing off badly from the smoother surface of the shell as shown.

VII An untreated shell with Ascidiella, Anomia, Pomatoceros, Balanus, and Laminaria: the rougher surface of the shell is shown.

Experiment E.

Shells of Pecten maximus *treated and strung on tarred ropes or nailed inside the raft at Cawsand Bay on August 18th,* 1919.

Observations were made on these shells at various times, and growth and resistance to growth found to occur in the order shown in experiments A to D.

One full report of the hanging shells was made on October 22nd, 1919, as in Table VII.

Table VII.

Report on Shells strung on Tarred Rope inside the middle compartment of the Cawsand Bay Raft.

		Growth on October 22nd, 1919 (exposed *c.* 9 weeks).
I	Reddish brown ; A–F 5 to 8 shells	None.
II	Green ; A–F 8 shells	None : 2 shells peeling.
III	Black ; A–C 5 to 8 shells	Large colonies of Tubularia with Nudibranch spawn and some Pomatoceros on all shells.
IV	Reddish brown ; A–F 8 shells	Five shells no growth : 2 shells with small growth and one with fair growth of Tubularia.
V	Black-bronze ; A–C 5 to 8 shells	All shells with large colonies of Tubularia and some Pomatoceros.
VI	Reddish brown ; A–F 5 shells	Three shells with only spawn of the Nudibranch *Facelina drummondi :* 2 shells with a little Tubularia.
VII	Greyish white untreated 5 to 8 shells	All shells have large colonies of Tubularia with Nudibranch spawn and some Pomatoceros.
VIII	Red ; A–C 8 shells	Seven shells with Tubularia and one clean : the paint is peeling off 3 shells.

History of the General Growth on the Raft in Cawsand Bay.

The history of the growth observed on and in the raft from time to time is important in relation to the growth found on the adjacent treated and untreated shells, and is best shown in a condensed form as follows in Table VIII.

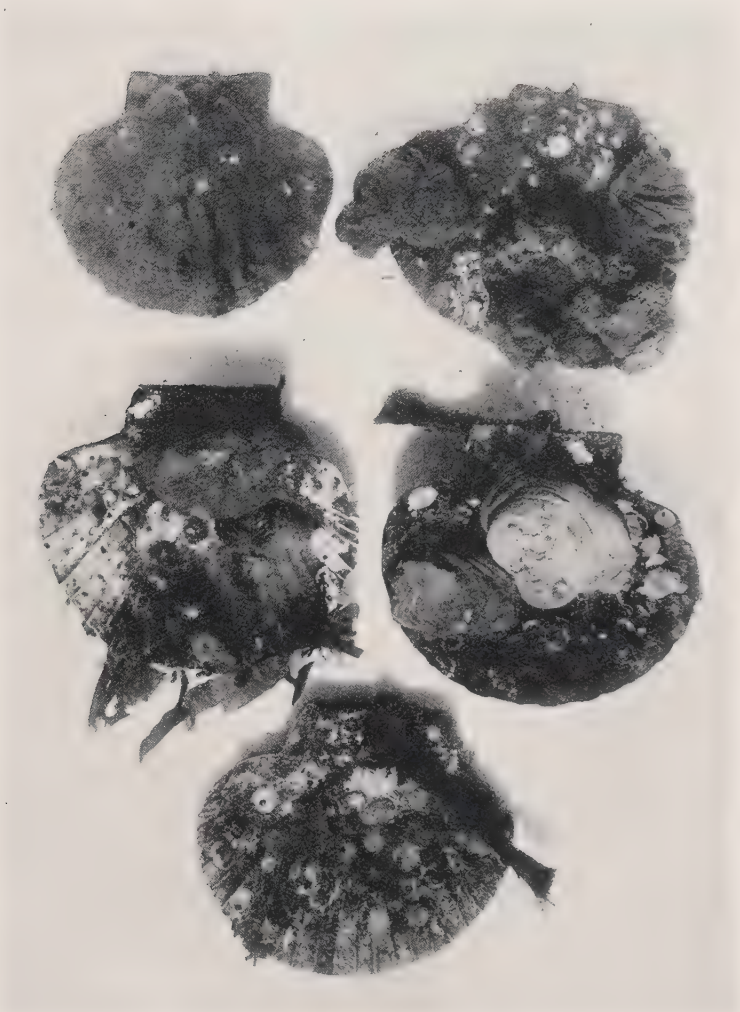


FIG. 10.—Photo of shells from Experiment D_1, Cawsand Bay Raft, October 9th, 1920. See Table V, p. 390. (× ca. $\frac{2}{3}$.) (Photo by D. P. Wilson.)

V Black. Outer (rough) surface of a convex valve with the paint still almost entire, but with Balanus, Anomia, Pomatoceros all becoming overgrown with Diplosoma.

VI Red: view of inner (smooth) surface of a convex valve almost denuded of paint, with a large Ascidiella, Dasychone, 15 individuals of Anomia, some Diplosoma, and several roots of Laminaria.

VIII Red: smooth surface of a flat valve now denuded of paint: with four large Ciona, 13 Anomia, one Balanus, some Diplosoma, and Tubularia.

III Black: inner surface (smooth) of a convex valve; with one large and one small Actinoloba, one large Ciona, several Hydroides, and Balanus, one Pomatoceros, one Anomia, and a little Diplosoma and Tubularia. The paint is almost entire and is being telescoped on the shells of the Balanus.

VII Untreated: inner smooth surface view: with Balanus, Pomatoceros, numerous Anomia, all becoming overgrown with Diplosoma, some Botryllus, Hydroids and a root of Laminaria.

Table VIII.

History of the Marine Growths on the Raft in Cawsand Bay, July 16th, 1919, to December 28th, 1920.

	Growth and remarks.
1919.	
July 16th	Raft put in the sea, tarred and dried, with attached pieces of untreated wood.
Aug. 7th	Obelia with spawn of Tergipes and *Galvina exigua* covering the bottom of the raft. Veligers already in the spawn. Teredo in borings about ½ inch long (perforated zinc crab-and-prawn cage put inside the raft).
Aug. 18th	Bottom of raft covered with dense growth of Obelia with great abundance of adult and spawn of *Galvina exigua* and *Tergipes despectus*. The Obelia being devoured by Nudibranchs. *Galvina picta, pallida,* and *farrani* types all common and a little Tubularia* obtained which extruded actinula larvæ overnight.
Sept. 30th	Large colonies of Tubularia common on the bottom of the raft, with abundant Pomatoceros and Nudibranchs.
Oct. 10th†	*Facelina drummondi* common on the raft up to a length of 3·6 cm. extended : numerous masses of its spawn on the large colonies of Tubularia, which at one end of the raft mostly have the " heads " eaten off.
Oct. 28th	The prawn *Leander* (=Palæmon) *serratus* has settled in numbers and grown *in situ* to a length of 4·3 cm. inside the perforated cage along with young *Cancer pagurus* which have a carapace diameter of 7 to 10 mm. Two fine colonies of Bugula (with ovicells and ova) in the perforated cage with Anomia, Tubularia, and Nudibranchs. The sides of the raft are covered with young Ciona. Tubularia and Nudibranchs still abound.
1920.	
March 2nd	Colonies of Membranipora sub-circular 4·5 by 5·0 cm. in diameter, and of Umbonula 2·2 cm. sub-circular. Anomia and Hydroides mature, and gave successful artificial fertilisations. Pomatoceros mature.
Oct. 9th	Small *Antedon rosacea* with arms to a length of 3·8 cm. and limpets, *Patella vulgata,* 8 to 13 mm. in length have settled on the raft ; the former below and inside, the latter on top and outside. Young *Pecten opercularis* up to 31 by 29 mm. in length and breadth have also settled and are sexually mature and gave good brown trochospheres in fair numbers on artificial fertilisation (a cross fertilisation was made in this case, *P. opercularis* is hermaphrodite). *Sabella pavonina* with tubes up to 17 cm. long by 4·5 mm. wide fairly common, and abundant adult Sycon and some Leucandra. The top of the raft is covered with Enteromorpha and some Ulva. (Put out on the raft fresh clean pieces of wood.)

* Tubularia was specially searched for on August 7th, and not seen : it is probable, therefore, that these small colonies grew in about eleven days.

† On this day a remarkable Galvina was taken : it had the characteristics of all three types—*picta, pallida, farrani*—in one individual. The lateral cerata were orange tipped ; the median, brown tipped, and the dorsal part of the body was splashed with reddish brown patches as is the case in *picta*.

FIG. 11.—Two shells from Experiment D_1, Cawsand Bay Raft, October 9th, 1920, with many large Laminaria fronds. (× ca. $\frac{1}{5}$.) (Photo by D. P. Wilson.)

The convex shell on the left was painted with No. VIII substance, red, which was almost all washed away from the inner (smooth) surface shown. On this shell, besides the Laminaria fronds, which have been folded, are one large Ascidiella, 13 Anomia, Pomatoceros, Hydroides, and Tubularia.

The convex shell on the right was painted with No. V substance, red, which remains only in traces on the smooth inner surface shown. Besides Laminaria, there are shown in this view of the shell, 4 large Balanus, 23 Anomia, one *Sycon coronatum*, and much Diplosoma. The larger fronds of Laminaria are folded along about half their length, and are themselves covered with numerous colonies of Diplosoma, some Botryllus and Obelia.

1920. Growth and remarks.

Oct. 23rd The raft is covered with Laminaria, and red weeds on the sides and green weeds on the top, but underneath and inside with animal growths. Samples of the growths were brought in to the Laboratory and examined as follows :—

Species.	Length of plant in cm.	Width of frond in cm.	Width of stipes in mm.	Remarks.
Laminaria saccharina	95	14	4	Frond frayed at end.
,, ,,	102	12	4	,, ,, ,, a little.
,, ,,	88	10	3·5	,, ,, ,,
,, ,,	110	16	4 to 6	Broken: possibly twice as long in uninjured condition.
,, ,,	143	15·6	8·5	Slightly broken.
,, ,, young	12·5	2·6 to 2·8	2 to 3	Entire.
,, ,, young	60	4·6	4 to 6	Entire.
L. digitata	83	32	8	Broken and covered with Membranipora on both sides.
L. digitata stipes and root	16	—	—	
,,	88	21	8·5	Frond broken.
,,	59	—	6·5	Frond broken with a colony of *M. membranacea* 25 × 5·5 cm. sub-rectangular.
,, young	23	—	3·8	Frond entire.
	29	—	5·5	,,

Helcion pellucida 6·8 mm. long was taken from the stipes of Laminaria and *Mytilus edulis* up to 24 mm. long were common among the roots of the same plants. There was a heavy growth of animals inside and at the bottom outside, the dominant forms being Pomatoceros, Anomia, Hydroides, Ciona, Ascidiella, Diplosoma, Balanus, Sycon, Podoceros (=Jassa), Tubularia, and other hydroids with various Nudibranchs and various Polyzoans. Among the less abundant and occasional forms were Sabella and other smaller Sabellids, Serpula, Pecten, Patella, Mytilus, Helcion, Antedon, Leucandra, Actinoloba *juv.*, Leander, Cancer *juv.*, Porcellana, and Carcinus *juv.*

1920.

Nov. 11th On this day the mooring chain and shackles were overhauled and made secure, as it was probable that it would be many months before observations on these experiments could be resumed owing to the investigator being called away on urgent work in connexion with oyster mortality (**4**).

Dec. 28th The raft broke adrift in a strong gale some time between the nights of December 25th and 27th, and was washed ashore ; it was badly smashed and rubbed. The whole of the top was missing and also many battens from the sides as well as all the experimental material. A reward was vainly offered for the discovery and return, especially of the experimental boards and the lid (for Patella). Apparently one of the main vertical bolts had broken in the wood, and its fellow had been broken off where it emerged from the wood. For this reason a stouter iron basic frame was introduced into future designs.

The battens on the bottom and sides were bored to a great extent by Teredo. Most of the borings were unoccupied and contained putrefying matter. Probably most of those belonged

to infections in previous seasons. A few borings of living animals were however found up to a length of 25 cm. with a mean diameter of about 1 cm. and a diameter of 12 mm. at the inner boring end. A few Actinoloba, Mytilus, Balanus, and Sycon remained on the raft. The Actinoloba are of interest as follows :—

Actinoloba dianthus.	Diameter of flower in cm.	Diameter of column in cm.	Diameter of base in cm.	Height of column.
(a) Pink and extended	9·5	4·3	5·5	—
(b) White contracted	—	3·8	3·2	2·7
(c) White partly extended	—	5·0	5·0	7·0
(d, e, f) Pink, 3 about same size as (a)				

The Exposure of the Raft and Experimental Material to "Infection."

The history of the growths on the raft and the experimental material in Cawsand Bay along with a knowledge of the breeding periods of the dominant organisms concerned render it possible to follow the exposure of the raft and experimental material to infection by potential growths.

When the raft was moored in the sea in Cawsand Bay it immediately became infected with Obelia planulæ and spores of Enteromorpha. Almost simultaneously Nudibranch post-veligers (of Tergipes and Galvina) attacked the young Obelia and established themselves. About August 7th, 1919, *Tubularia larynx* actinulæ settled on the raft and established a recurring source of infection which was maintained until the close of the experiment. Thus when the experimental material was put in the sea on August 18th, 1919, it became subject at once to infection by Tubularia from at least a local source. The larval form of Tubularia, the actinula, is highly adhesive ; and it will adhere firmly to a clean glass pipette or dish, or to the frond of Laminaria, and very easily to rougher surfaces than these. This larva is moreover virtually a passive floating organism, it is devoid of light-sensitive organs, and is thus one of the most efficient larvæ for testing the value of a poisonous surface. Indeed, both the efficiency of the poisonous paints and of the larva as well as that of the infection is demonstrated in experiments A to E by the fact that this larva established itself on all the non-poisonous surfaces and on small rubbed areas of the shells painted with proven poisonous paints.

During August numerous Pomatoceros and Diplosoma larvæ settled on the raft and on the shells treated with non-toxic paints. Diplosoma, like Tubularia, produces larvæ, in this case, however, tadpoles, which are adhesive and settle at once on objects adhered to. It is probable that the tadpole of Diplosoma is only light-sensitive for a short space of time, if it is at all light-sensitive. Diplosoma can attain maturity in six weeks and breeds during most of the year, so that once this organism is

established on a locality it can reinfect the locality over the greater part of the year, excepting the winter period.

In this month, August, and in September the larvæ of Ascidiella and Ciona settled in numbers on the raft along with the larvæ of Balanus, Teredo, Sponges, Polyzoa, and Polychætes, and the spores of many seaweeds.

There is little doubt that infection from all the sources would continue during October and at least part of November (2).

After November general infection would diminish until about March–April, when a fresh infection of Balanids and Hydroids especially would begin, and from April–May onwards all the dominant forms mentioned above would continue to infect the raft from outside and some from local sources during the ensuing summer. There can be no doubt, therefore, that the experimental material on the raft was well tested by a succession of larvæ during the greater part of the time that the raft was in the sea, as is shown by the general growth on the raft itself.

Results of Experiments A to E.

Under the conditions of these experiments, which are in some respects severe (but see general discussion on p. 428), it is seen that only the substances II, IV, and I have an effective anti-fouling action. During the period of these experiments, i.e. about fourteen months (August to October), so long as these paints remained on the experimental material, animal growth was almost entirely inhibited by these three substances, but where they were exposed to light growth occurred in about six months. The substances II, IV, and I adhered to the test material approximately in this experiment in the order of their value for inhibiting animal growths, so that it is probable that the paints were eroded before losing their toxic value.

It is thus manifest that a fundamental property of an anti-fouling paint is the capacity for resisting rapid erosion or dissolution in the sea. In these tests all the experimental material was subject to the constant movement produced on the raft by wind and waves.

The anti-corrosive paints III and V remained in the best condition on October 23rd, 1920, and may therefore be said to fulfil a preservative function (for non-wooden structures) satisfactorily for the period and conditions of the experiments.

Red oxide of iron, No. VIII substance, which is commonly used as an anti-corrosive paint on iron buoys, was found to be useless as an anti-fouler; and since it became eroded almost entirely in fourteen months, or less, must be deemed less valuable as an anti-corrosive paint than substances III and V for the conditions of these experiments which are similar to those affecting buoys.

SERIES II. GREAT WESTERN RAILWAY, WEST WHARF, MILLBAY DOCKS, PLYMOUTH.

Experiment F.

On 3-feet test-boards fixed at low-water mark.

In this experiment eleven boards 3 feet by 4 inches by 1 inch were treated with substances I to XII (see p. 376) excepting No. VII board, which was again untreated—and put in the sea on August 27th, 1919. These boards were affixed vertically to old Jarra piles at low-water mark at the West Wharf, Millbay Docks, Plymouth. The lower ends of the boards (except No. II, which was slightly higher than the others) were fixed about 6 inches below ordinary spring-tide level so that about 2 feet 6 inches of the board would be above the mean spring-tide level. Four additional untreated pieces of wood were put out as additional controls of growth on August 28th, 1919, and five more pieces of untreated wood were put out on February 23rd, 1920, alongside the experimentally treated boards in Bays 3 to 7 inclusive, i.e. alongside boards VIII and XII, V, IV, IX, and XI. These untreated boards were soon lost, but they served the purpose of demonstrating growth on untreated surfaces alongside the treated surfaces. Substances VIII, red oxide of iron, and XII, aluminium paint, were painted on to one board on vertical halves (36 by 2 by 1 inches). The 3-feet boards were of red pine, except No. VII, which was of elm, the additional pieces of wood being ordinary deal.

Numerous visits were made to the West Wharf in studies on the low-water fauna, and the records made on ten inspections of the experimental material from September 25th, 1919, to March 7th, 1923, are given in Table IX, pp. 402–3. In this table is shown the history of the growths which occurred on each of the boards and the condition of the paint. The growths on the experimental substances and on untreated wood (VII) can be readily and easily compared at successive periods of the experiment. The condition of the surviving boards at the end of the experiment is shown in Figs. 12, p. 404, 13 and 14, pp. 405 and 408.

Summary of Results from Experiment F.

The board with the green poisonous paint, No. II, remained almost intact during the course of the experiment, i.e. about $3\frac{1}{2}$ years. All the remaining surviving boards were badly eaten by gribble at the close of the experiment, and of the two boards which were lost, one (No. XI) was nearly eaten away on December 16th, 1921, but the other (No. IX) on this latter date was in good condition and might have remained so for a longer period.

Growth began first on boards V and IX. It is a noticeable fact that

TABLE IX. EXPERIMENT F.

REPORTS ON GROWTHS (AND CONDITION OF PAINTED SUBSTANCE) ON 3-FEET TEST-BOARDS (TREATED AND UNTREATED) PUT OUT ON AUGUST 27TH, 1919, AT LOW WATER SPRING-TIDE LEVEL AT THE WEST WHARF, MILLBAY DOCKS, PLYMOUTH.

No., colour, and designation of paint and position of board.	Sept. 25, 1919 (exposed *c.* 1 month).	Dec. 8, 1919 (exposed *c.* 15 weeks).	Feb. 7, 1920 (exposed *c.* 6 months).	May 19, 1920 (exposed *c.* 9 months).	Aug. 16, 1920 (exposed *c.* 12 months).	April 22, 1921 (exposed *c.* 20 months).	Dec. 16, 1921 (exposed *c.* 28 months).	March 17, 1922 (exposed *c.* 31 months).	March 7, 1923 (exposed *c.* 42½ months).
I Reddish brown A–F 10 Bay	No growth	No growth, paint good	No growth, but an untreated board alongside has Diplosoma and Botryllus	No growth, paint good	Slight growth of a few barnacles: paint washing off. (Untreated board alongside covered with growth and riddled with gribble)	Slight growth on bottom of board; on the lead label and on a nail head; no gribble seen	A little growth only on the bottom of the board	Not reported on	Good piece of board still left and *brought in*. One-third eaten away by gribble: bored by Teredo. The faces of board mostly eaten also by gribble, but the little paint left is overgrown by Botryllus and other organisms. See fig. 13
II Green A–F 11 Bay, outer	No growth	No growth, paint good	No growth, paint good	No growth, paint hard and in good condition	No growth: paint good but soft and rubs off on the finger; washed off a little in a few places at the sides	No growth: a little on a nail head, no gribble seen	No growth	Not reported on	Slight growth only in places, and attacked by gribble isolated parts and at edges. *Board brought in* still covered with some paint on most of surface. See fig. 13
III Black A–C 11 Bay, inner	No growth	No growth, paint good	No growth, but has spawn of Eulalia on it	Good growth, covered at bottom: paint very good and hard (Clean board alongside covered with growth and riddled with gribble)	Covered with growth	Extensive growths all over, no gribble seen	Not examined	Not reported on	Good piece of board left, but covered by by growth. Board *brought in*. See fig. 13, p. 405
IV Reddish brown A–F 5 Bay	No growth	No growth, paint good	No growth	A few barnacles on the bottom of the board; paint very good (Untreated board alongside covered with growth and riddled with gribble)	Slight growth of a few barnacles; a little Diplosoma and Bugula Sept. 30, 1920. Botryllus on lead label, and a few colonies of Botryllus on the board	Slight growth of hydroids, Balanus and Sycon No gribble seen	A good growth now present	Not reported on	Good piece of board left, but covered by growth. *Board brought in*, paint still covering part of surface. See fig. 13, p. 405
V Black-bronze A–C 4 Bay	Growth begun, small colonies of Diplosoma and a growth of Obelia	Good growth, fewer Diplosoma; Botryllus, Ficulina, and much hydroid growth, paint good	Good growth of Diplosoma and Halichondria on the bottom of the board	Covered with growth of small colonies of Diplosoma and Obelia: paint very good (Untreated board alongside as in III and IV)	Covered with growth of Diplosoma, Botryllus, Balanus, Bugula. Untreated board alongside riddled by gribble	Extensive growth: board eaten by gribble about ½ inch at the sides	With a good growth, nearly eaten away by gribble	*Now eaten away to a small remnant and brought in.* See fig. 14, p. 407	

VI Reddish brown A–F 12 Bay	No growth	Not examined, tide too high	No growth, paint rubbing badly and apparently brighter red in colour	Growth of hydroids and Ascidians	Covered with growth everywhere: paint washing off and very soft	Heavy growth of Balanus: moderately eaten by gribble on the face as well as at edges	Now partly eaten away and covered with growth	Not reported on, but on April 29, 1922, found to be *nearly eaten away by gribble and brought in.* See fig. 14, p. 407	
VII Greyish white untreated 14 Bay 8 Bay outer and inner 3 to 7 Bays	No growth	Good growth on two boards, three boards not seen. Diplosoma, Botryllus, Umbonula and hydroids	All untreated boards with Diplosoma and Botryllus and gribble, especially on the bottom of the boards	Covered with growth, and board becoming riddled with gribble. Teredo probably also present	Covered with growth and riddled with gribble	*Nearly eaten away and brought back to laboratory.* Two additional untreated boards previously riddled with gribble are now missing, doubtless having broken away after being reduced to a remnant. See fig. 14			
VIII Red A–C 3 Bay	No growth	No growth, paint now washing off	No growth visible	Covered with spat of Balanus: paint very soft	Covered with growth of Diplosoma, Botryllus, Bugula, Balanus, and Limnoria, and on July 15 had also some brown algæ	Extensive growth: one half of the board eaten (north side) by gribble	With a good growth and nearly eaten away	*Now eaten away to a small remnant and brought in*	
IX Black A–C ? 6 Bay	Growth begun by a young colony of Halichondria sp.	Much Diplosoma on bottom of board and some Ascidians, paint good	Much growth of Diplosoma and Botryllus on the bottom of the board	Good growth covered with spat of Balanus, hydroids and Ascidiella: paint very good	Covered with growth as on VIII and also medium Ascidiella	Extensive growth: slight attack by gribble in one corner only	Covered with growth; not much eaten by gribble	Not reported on	LOST
X Black A–C 9 Bay	No growth	Slight growth, paint good	Growth of Diplosoma and Botryllus	Covered with growth and spat of Balanus at higher level: paint very good	Covered with growth, paint in good condition	Extensive growth: not attacked by gribble except in one top corner	Covered with growth, gribble is beginning to eat away the top part of the board	Not reported on	Most of the board still left, and paint remains on nearly half of outer and most of inner face. Covered with growth and *brought in.* See fig. 13, p. 405
XI Green A–F 7 Bay	No growth	No growth, paint good, Halichondria near board apparently unable to overgrow on to it	No growth, Halichondria in juxtaposition to board in places but is unable to grow on to board	Much spat of Balanus, but no hydroids seen; paint very good. (clean board alongside, put out Feb. 23, covered with growth and riddled with gribble)	No paint left; growths extending all over board (July 15 paint nearly all washed off, fair growth on bottom of board)	Fair amount of growth: moderately eaten by gribble in patches	Nearly eaten away by gribble	Not reported on	LOST
XII Silvery grey 3 Bay	No growth, paint cracking	No growth visible: paint good except for cracks	No growth visible	Covered with spat of Balanus: paint still fairly hard	Covered with growth	Extensive growth: one half of the board eaten by gribble	Nearly eaten away by gribble	*Now eaten away to a small remnant and brought in*	

NOTES TO TABLE IX. EXPERIMENT F.

The Bays in which the boards were put out are reckoned from the south end of the West Wharf.

On December 16th, 1921, the examination of the boards was made in my absence by my assistant in this work, Mr. William Searle.

Paints VIII and XII were painted on the same board, half of the board on the long axis and $36 \times 2 \times 1$ inches being painted with red oxide and the corresponding half with aluminium paint.

"Gribble" is a seaman's term for both *Limnoria lignorum* and *Chelura terebrans*. Both these animals were taken from the experimental material, but Limnoria was by far the most abundant, and appears to live at a slightly higher level in the inter-tidal zone than Chelura.

As the boards were nailed on to and against Jarra piles, it was not possible to examine the back parts of the boards during the course of the experiments

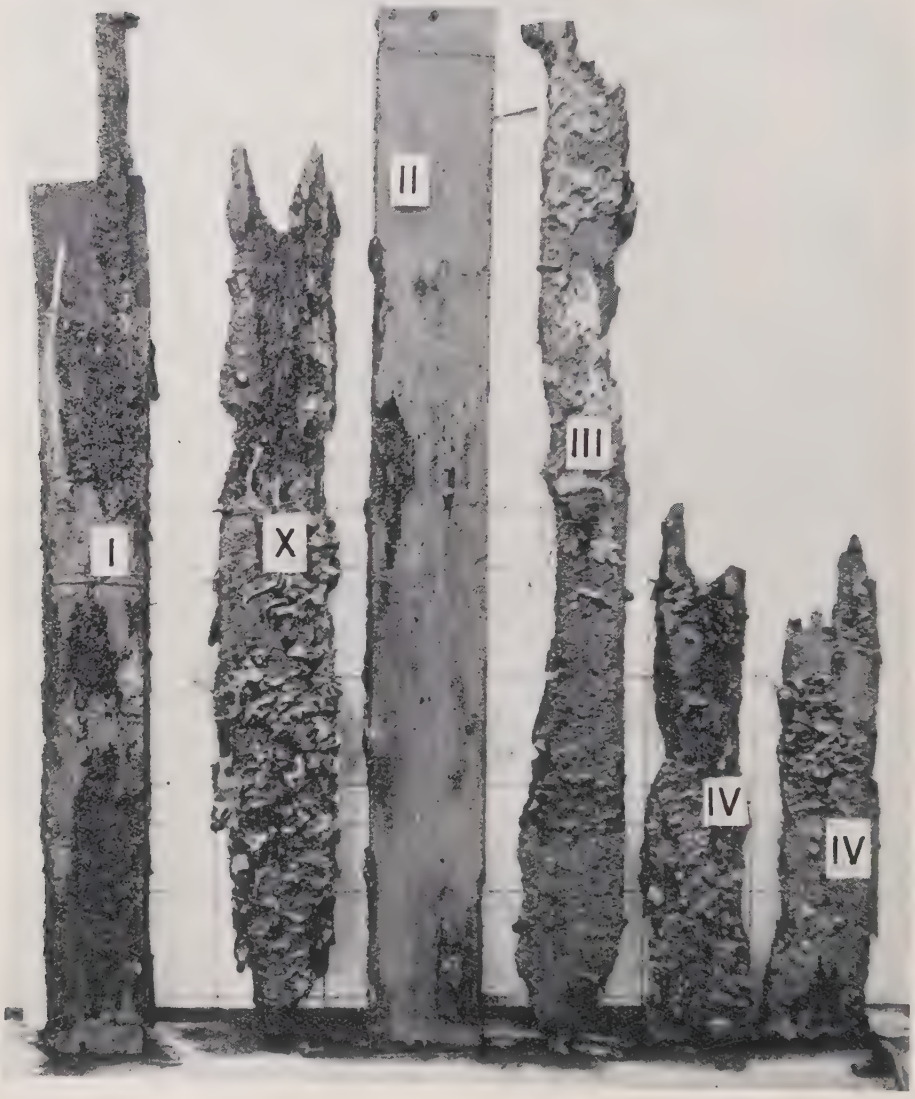


Fig. 12.—Photo of test-boards from Experiment F, Great Western Railway Wharf, Millbay Docks, Plymouth, with living growths on March 7th, 1923, after 3½ years' exposure in the sea. ($\times \frac{2}{13}$.) (Photo by A. J. Smith.)

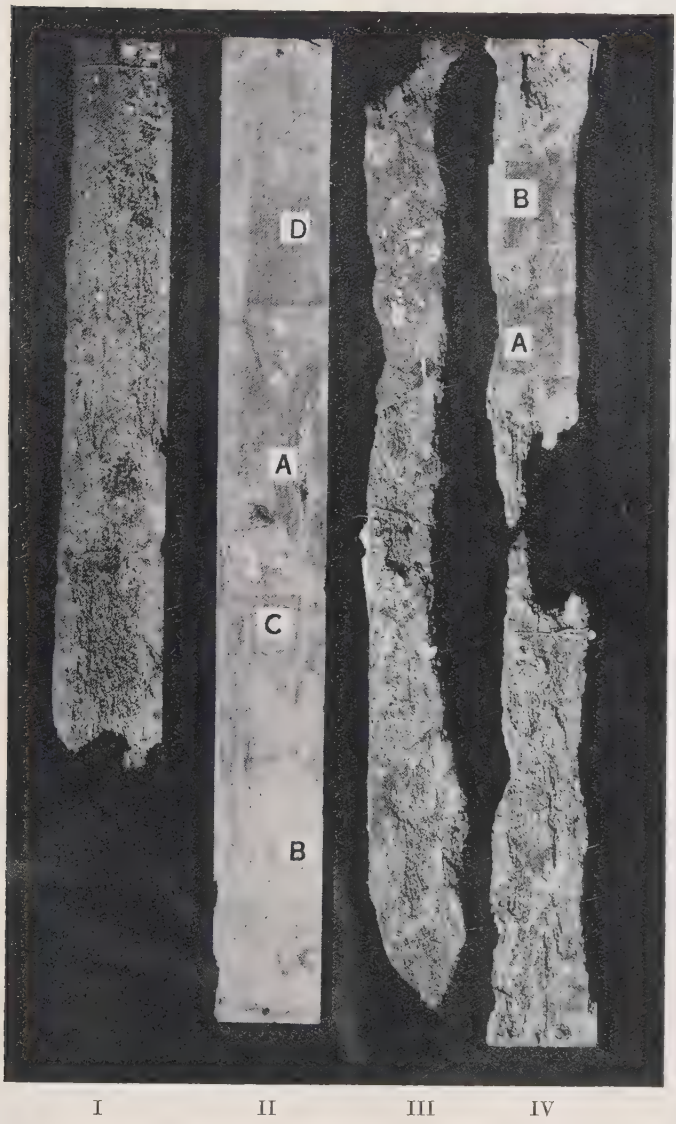


FIG. 13.—Photo of test-pieces from Experiment F, Great Western Railway Wharf, Millbay Docks, Plymouth, dried after exposure in the sea for $3\frac{1}{2}$ years from August 27th, 1919, to March 7th, 1923. (× ca. $\frac{1}{7}$.) (Photo by D. P. Wilson.)

Test-piece No. I has had a small portion and the end of a Teredo tube broken off (see Fig. 12, p. 404).

Test-piece No. II shows the four areas B, C, A, and D (in order from below upwards) from which samples of paint were scraped for chemical analysis.

Test-piece III is shown from the side opposite to that shown in Fig. 12, p. 404.

Test-piece IV shows the two areas, A and B, from which samples of paint were scraped for chemical analysis (compare IV, fig. 12, p. 404).

this growth occurred while the untreated board remained devoid of growth. There is little doubt that all kinds of wood are liable to be slightly inimical to growths (and perhaps toxic) for a short period (i.e. a few weeks) after being put into the sea. The untreated board No. VII —comparable with the experimental boards—however, became covered with growth (after 15 weeks in the sea) and was eaten away to a remnant in 20 months. Four other boards, V, VI, (VIII and XII) and XI were eaten away to a remnant in 31 to 32 months, and four others, IV, I, III and IX became badly eaten away—though not reduced to a remnant—in $42\frac{1}{2}$ months, while as stated above No. II board remained almost intact at the end of the period of $42\frac{1}{2}$ months. (See Figs. 12, 13, and 14.) It is therefore possible to estimate the *preserving* action on wood of the substances which were tested by taking as a basis for comparison the length of time required for the destruction of the untreated test-piece of wood, namely No. VII. In this way are derived the estimates of the preserving action shown in Table X, below. The value of each substance for inhibiting growth can be deduced from Table IX in a similar way, and is best shown in tabular form as in Table XI, p. 409.

Table X.

Rate of Destruction of the Test-Boards and the Deduced Preservative Value of the Substances Tested on Wood in Experiment F, Millbay Docks, Plymouth.

No. of test-board and substance.	Date eaten to remnant or brought in.	Months in which test-piece eaten to a remnant (approx.).	Actual and estimated* periods for reduction of all test-boards to a remnant in months (approx.).	Value of preservative action in months (approx.).	Experimental poisonous or other substance.
VII	April 22nd, 1921	20	20	—	Untreated.
V	March 17th, 1922	31	31	11	Black-bronze : anti-corrosive.
VIII	,,	31	31	11	Red oxide of iron : anti-corrosive on iron.
XI	,,	31	31	11	Green : anti-fouling paint.
XII	,,	31	31	11	Aluminium paint experimental.
VI	April 29th, 1922	32	32	12	Reddish brown anti-fouling paint.
IX	Lost	28+a	*49*	29	Black : ordinary black varnish.
IV	March 7th, 1923	$42\frac{1}{2}$+b	*49*	29	Reddish brown anti-fouling paint.
X	,,	$42\frac{1}{2}$+c	*49*	29	Black : ordinary coal tar.
I	,,	$42\frac{1}{2}$+d	*49*	29	Reddish brown anti-fouling paint.
III	,,	$42\frac{1}{2}$+e	*49*	29	Black : anti-corrosive paint.
II	,,	$42\frac{1}{2}$+f	*65*	45	Green : anti-fouling paint.

* Estimated periods are given in italics.

An inspection of Table X brings out the somewhat surprising fact that the black-bronze anti-corrosive paint (V), the green anti-fouling paint (XI), red oxide of iron (VIII), and aluminium paint (XII) all have an approximately equal value as preservative substances under the condition of the experiment. The red anti-fouling paint (VI) was only a little better than the preceding substances. The failure of these substances to preserve the test-boards is undoubtedly due to the readiness in which they become eroded off the test-boards, while the similarity in the rate of erosion suggests that the body used in these paints was essentially similar.

The substances IX, IV, X, I, and III were approximately equal in preserving value, and owed their increased value undoubtedly to their property of resisting erosion. It is a striking fact that ordinary coal-tar (X) and ordinary black varnish (IX, i.e. coal-tar diluted with naphtha) are as good preservatives as the more expensive paints III, IV, and I under the conditions of these experiments.

The green anti-fouling paint (No. II) stands out in these experiments as a very efficient preservative and—as will be shown later –also a very valuable anti-fouling substance. A similar preservative value to that deduced above would be obtained by taking the relative condition of the boards on December 16th, 1921, after 28 months in the sea (see Table IX, p. 402).

The relative anti-fouling value of the substances tested in this experiment can be estimated approximately from the data given in Table IX. The dates at which general growth was first observed on each test-board gives the approximate time at which the anti-fouling value (if any) of each substance was lost. The intervals of observation are too widely spaced to give in most cases the date at which slight general growth occurred, but in the period between observations recording no growth (or slight growth) and general growth must have occurred the onset of general growth. This period in the case of each test-board is shown in Column 3, Table XI, p. 409. By taking the middle of this period, i.e. between the occurrence of no—or slight—growth and general growth, an approximate date is obtained for the onset of general growth, and this is given in column 4, Table XI. Since substances V and IX showed slight growth in one month, these may be safely stated to have no anti-fouling value (confirmed in other experiments), and the period required in the case of these two substances for the onset of general growth may be taken as the zero for the determination of the relative anti-fouling value of each substance. The relative values obtained in this way are given in Table XI, column 5. A detailed description of the boards recovered from the sea on March 7th, 1923, is given on pages 410–13.

FIG. 14.—Photo of remnants of test-pieces from Experiment F, Great Western Railway Wharf, Millbay Docks, Plymouth, dried after various periods of exposure in the sea.($\times \frac{1}{7}$.) (Photo by D. P. Wilson.)

All the test-pieces were first exposed in the sea on August 27th, 1919. No. V test-piece remnant was taken out of the sea in March, 1922; No. VI in April, 1922; No. VII in April, 1921, and No. X in March, 1923.

Table XI.

Rate of Infection of the Test-Boards in Experiment F with General Growth; and the Deduced Anti-Fouling Value of the Substances Tested (on Wood).

(1) No. of test-board and substance.	(2) Incidence of slight growth in months (approx.).	(3) Incidence of general growth in months (approx.).	(4) Time taken to establish general growth in months (approx.).	(5) Relative anti-fouling value in months (approx.).
V	1	1–2¾	1½	0
IX	1	1–2¾	1½	0
VII	—	1–2¾	1½	1
X	2¾	2¾–6	4½	3 (0)†
III	—	6–9	7½	6 (0)‡
VI	—	6–9	7½	6
VIII	—	9–12	10½	9
XI	—	9–12	10½	9
XII	—	9–12	10½	9
IV	12–20	20–28	24	22½
I	12–28	28–*36**	32	30½
II	28 nil	*36*–42½**	39	37½

Table XII.

Comparative Anti-Fouling and Preservative Values Deduced from Experiment F.

No. of sub-stance.	Colour and property.	Deduced anti-fouling value (in months).	Deduced preservative value (in months).	Property found in Experiment F.
CLASS A.				
II	Green: anti-fouling	37½	45	A.F. and pres.
I	Reddish brown: anti-fouling	30½	29	A.F. and pres.
IV	Reddish brown: anti-fouling	22½	29	A.F. and pres.
CLASS B.				
IX	Black (varnish): experimental	0	29	non A.F. but pres.
X	Black (coal-tar): experimental	3 (0)	29	non A.F.† but pres.
III	Black: (anti-corrosive and preservative paint)	6 (0)	29	non A.F.‡ but pres.
CLASS C.				
V	Black-bronze: anti-corrosive	0	11	non A.F.: sl. pres.
VI	Reddish brown: anti-fouling	6	12	sl. A.F.: sl. pres.
VIII	Red (oxide of iron): experimental	9	11	sl. A.F.: sl. pres.
XI	Green: anti-fouling	9	11	sl. A.F.: sl. pres.
XII	Aluminium paint: experimental	9	11	sl. A.F.: sl. pres.
CLASS D.				
VII	Untreated wood: greyish white	1	0	very sl. A.F. non pres.

* The figures in italics are estimated. ** General growth on bottom of board only.

† See Experiment G, p. 415, and fig. 16, p. 414, for rapid overgrowth.

‡ See Experiment G, p. 415, and fig. 15, p. 412. No. III substance was tested in No. II inner bay, all the others being placed in outer bays, and was doubtless subjected to a lesser degree of infection in this situation. See also Table XV, p. 422, for rapid overgrowth.

The Anti-Fouling and Preservative Values Deduced from Experiment F.

The estimated anti-fouling values (in months) deduced from Experiment F in Table XI, p. 409, and of the deduced preservative value (in months) in Table X, p. 406, for the various substances tested in this experiment are presented together in Table XII, p. 409. From this table it is seen that the substances fall naturally into four groups or classes as shown.

The results shown in Table XII are discussed on p. 426, after the consideration of experiments on painted shells, which were put out in the sea near the test-boards of Experiment F.

Biological (and Chemical) Observations on the Test-Boards in Experiment F after $3\frac{1}{2}$ Years' Exposure in the Sea.

After the test-pieces in Experiment F had been in the sea for $3\frac{1}{2}$ years the remaining boards were brought in to the Laboratory and photographed. Two of the boards, Nos. II and IV, were sent to the Government Chemist, London, for chemical analysis of samples of the paint in the condition of (*a*) permitting over-growth, and (*b*) apparently in the last stage of inhibiting growth. A report of these and other chemical analyses are given in Part II on pp. 430 to 437, and a discussion of the results obtained is given on pp. 438 to 441.

Biological Observations

No. II. Dark green anti-fouling paint.

The board retained its original size (see Fig. 12, p. 404). The front *face* of the test-board had a slight growth of hydroids in a small area (area A, Fig. 13) around the fixing nail in the middle and at one side. There was also a growth of hydroids on the lead (identifying) label on the top of the board. More or less paint was present on all the face except the lower six inches where were colonies of Diplosoma, Umbonula, and hydroids. There was no other growth on this face (Areas C and D, Fig. 13), but about 8 inches from the bottom in the middle of the face (Area B, Fig. 13) were four recent isolated borings of Limnoria (or Chelura). A few gribble borings were also present on the bottom of the board and around the middle fixing nail.

On the back *face* of the board paint still remained on the major part, but was missing from the lower 6 inches where Diplosoma and Halichondria were growing, and a few places where it had rubbed against the jarra pile. An area near the bottom of the board was eaten out by gribble over a surface of about 2×1 inches and to a depth of 1 cm., and another area $5\frac{1}{2}$ by $1\frac{1}{2}$ inches was similarly eaten out on the back of the board around the middle fixing nail. But there was no other growth on the face.

At one *side* ($36 \times 1 \times 1$ inches) of the board the paint had almost disappeared and gribble had attacked most of one edge, but little of the other except at the bottom.

On the other *side* some paint remained except on the bottom $5\frac{1}{2}$ inches.

On the upper part of both the *sides* hydroids were growing abundantly with some Botryllus and Polydora; while Diplosoma, Botryllus, Halichondria, and Polydora and gribble occurred on the lower parts. Limnoria and Chelura were taken from many places, but only in the lower three-fourths of these sides of the board. The top and bottom faces ($4 \times 1 \times 1$ inches) of the boards were intact.

No. I. Reddish brown anti-fouling paint.

The lower 9 inches of the board were missing, having probably been eaten away. The upper portion (see Fig. 12, p. 404) had only patches of paint left on either the front or back face. In places where traces of the paint remained it was distinctly overgrown with Botryllus, Umbonula, and Polydora tubes. A specimen of Teredo, with a tube 18 cm. long (slightly broken), remained projecting from the test-piece; the wood originally surrounding this tube having been eaten away by gribble. A large part of the face of both the front and back had been eaten away by gribble, and on the front face now were growing in abundance Polydora, Botryllus, Diplosoma, Balanus, and hydroids; on the back were present the same organisms excepting Balanus. From the bottom of the board a sample of 50 gribble was examined and found to be *Chelura terebrans*, and at the top, among about 20 to 30 specimens, only a few were Limnoria.

No. IV. Reddish brown anti-fouling paint.

The test-board was eaten away in the middle, leaving two pieces (see Fig. 12, p. 404). The upper portion, 16–17 inches long, was eaten away at the sides to a width of $3\frac{1}{4}$ inches. There was a good covering of paint over the outer face of the wood (of which Areas A and B were scraped and analysed chemically, see p. 434). The painted surface was unbroken in Area B, but perforated by Limnoria (or Chelura) in Area A, see p. 405, but was covered with a growth of Botryllus, Balanus, Umbonula, and Polydora, Pomatoceros and hydroids, especially a species of Obelia. The wood had been attacked by gribble in such a way as to leave in places a thin surface lamina covered by paint, a fact demonstrating the persistent, poisonous nature of the paint. The back surface of the wood (adjacent to the jarra pile to which it was fixed; and also remote from light) was eaten away over nearly the whole extent, probably having been undermined more quickly than on the front surface. The same kind of growth was found on the back as on the front.

The lower portion of the board also had a covering of paint still remaining over a good part of the front surface, but very little over the back. The paint on the front face was, however, overgrown very much with Botryllus and Diplosoma, several individuals of Balanus, and some Leucosolenia, Botrylloides, Polydora, and hydroids, and a pink sponge, probably a small colony of Hymeniacidon sp. Similar growth occurred at the back face, namely, Botryllus, Botrylloides, Diplosoma, but also Anomia and Umbonula.

No. X. Ordinary coal tar.

The board was almost entire, but eaten away by gribble around most of the original edges (see Fig. 12, p. 404). Paint still remained on nearly half of the outer—and mostly upper—face, and was in excellent condition on most of the back face. On the outer face the lower half was eaten away by gribble on the surface and almost to a point from the lower sides. Growing on the paint in the upper part of this face were Halichondria, Botryllus, Diplosoma, Hymeniacidon, Morchellium, Actinoloba (brown), and a fair amount of worms. On the back face were growing Halichondria, Botryllus, Diplosoma, Umbonula, Pomatoceros, Balanus, Anomia, hydroids, and a few Sabellid worms.

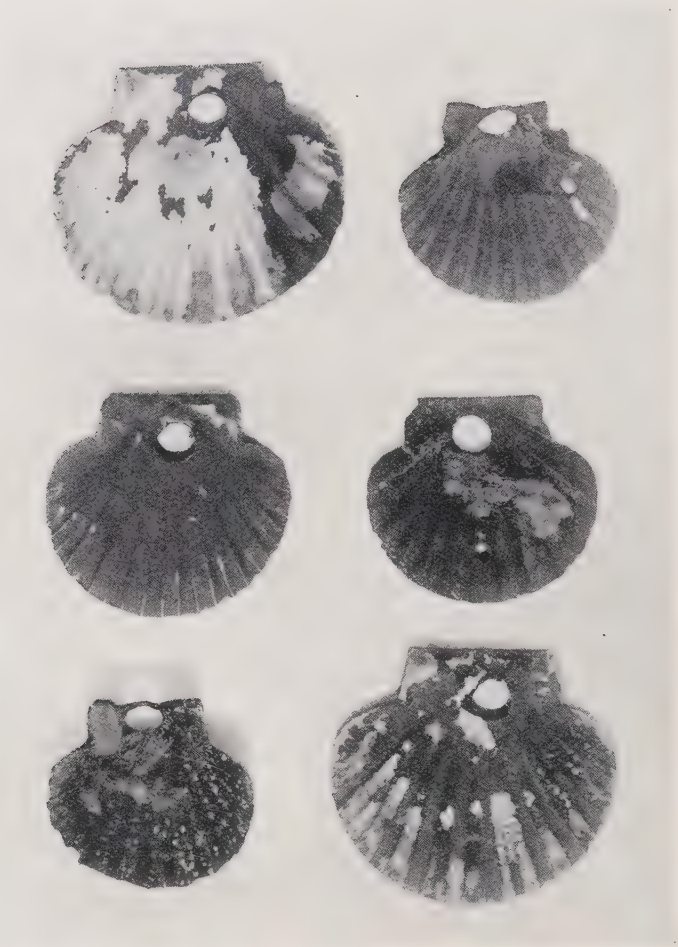


FIG. 15.—Photo of shells exposed at the Great Western Railway Wharf, Millbay Docks, Plymouth, Experiment G, from August 28th, 1919, to May 4th, 1920. (× ca. $\frac{2}{5}$.) (Photo by D. P. Wilson.)

I Red: view of inner smooth surface of a flat shell showing the paint washing away but devoid of growth. (The paint on rough surface—not seen—is almost entire.)

II Dark green: view of inner smooth surface of a flat shell, which is losing paint only at the right-hand upper corner and on certain ridges. There is no growth on this shell. (The paint on the rough surface—not seen—is almost entire.)

III Black: view of inner smooth surface of a convex shell showing the layer of paint to be entire. There is a growth of Halichondria, Leucosolenia, and a hydroid, and a good spatting of Balanus. (The paint on the reverse surface is also entire.)

IV Red: view of inner smooth surface of a convex shell showing the layer of paint to be almost entire. There is no growth on this shell. (The paint on the reverse surface is also almost entire.)

V Black-bronze: view of outer rough surface of a flat shell showing the paint entire and a growth of Ascidians, hydroids, Balanus, and young polychætes. (The inner smooth (reverse) surface shows a slight denudation of paint.)

VI Red: view of inner smooth surface of a flat shell showing the paint denuded from considerable areas and the spatting of Balanus on the bare shell and on the areas still retaining paint. (The paint on the reverse rough surface is almost entire.)

No. III. Black : anti-corrosive and preserving paint.

The test-piece retained the original length of about 3 feet, but was badly eaten away from one edge. An original edge on half of one side remained with paint on it and was only slightly bored by gribble (see Fig. 12, p. 404). The front face along the middle of its length had paint still adhering in very good condition, but was covered everywhere with growth. At the top of the face was much Diplosoma and Botryllus, a few Ascidiella and Botrylloides and a fair amount of encrusting Polyzoan : in the middle was very much Halichondria and Umbonula and a fair amount of Botryllus and Diplosoma, one Pomatoceros, and hydroid colonies : on the bottom of the front face was a lot of Botryllus and Umbonula, a little Diplosoma and a fair amount of the small Sabellid.

On the back face of the board, which was much more eaten by gribble than the front, where the paint remained, it was in good condition ; there was a growth of Sabellid tubes everywhere, eight Balanids, one Anomia, one Pomatoceros, and a little Botryllus and Halichondria.

Experiment G.

Shells of the scallop, *Pecten maximus*, were painted (in lots of ten) with the substances I to XII (see p. 376) (except No. VII, which is as in all the experiments—untreated material) and put out on tarred rope around the cement supporting piles of the West Wharf, Millbay Docks, Plymouth, on August 28th, 1919, at low water spring-tide level. Two shells of each of the twelve kinds were strung round each of the following piles, counting from the south end of the south division of the wharf :— 4th row 2nd pile (=4 R 2 P), 5 R 2 P, 6 R 2 P, 7 R 2 P, 8 R 2 P ; while on 9 R 2 P were strung a number of shells, all of which were clean, or rather untreated. The 4th row of piles separates the 3rd from the 4th bays, and the 5th row separates the 4th and 5th bays, and so on. Th experimental material in Experiment F was put out on jarra piles in bays 3 to 14 adjacent to the cement piles (about 2 yards distant) used for this experiment. Thus the sites in the two experiments were essentially similar though the upper half of each test-board would be above the level of the shells ; the shells would be also rather more shaded from light than the boards, and about 1 yard further from the small beach, which is exposed at low water at the back, i.e. inner part, of the wharf.

Observations on this experiment were only carried out over a period of 19 months (owing to the absence of the investigator on other work), but the period was sufficient to discover most of the results obtainable from an experiment of this kind. An examination of and report on individual shells was made on four inspections and general observations made on others. These observations are summarised in Table XIII, p. 415, and the results of the experiments are shown on Figs. 15 and 16, pp. 412 and 414.

Fig. 16.—Photo of shells exposed at the Great Western Railway Wharf, Millbay Docks, Plymouth, Experiment G, from August 28th, 1919, to May 4th, 1920. (× ca. $\frac{2}{5}$.) (Photo by D. P. Wilson.)

VII Untreated shell: view of inner smooth surface of a flat valve with a slight growth of Halichondria, much hydroid growth and spat of Balanus with also young tubicolous Sabellid polychætes. The growth on the reverse rougher side is similar.

VIII Red: view of inner smooth surface of a flat shell showing areas denuded of paint, Balanus spat on the paint, and a slight growth of tubicolous polychætes around the larger hole. On the rougher reverse side the paint is practically entire, but with similar growth.

IX Black: view of inner smooth surface of convex valve showing the paint almost entire, a good growth of Halichondria, hydroids and Balanus, and a few tubicolous polychætes. The reverse side is similar.

X Black: view of inner smooth surface of a convex valve showing the paint almost entire, a good growth of Botryllus, Diplosoma, and Balanus. The reverse side is similar without Diplosoma.

XI Light Green: view of inner smooth surface of convex valve showing large areas denuded of paint and no growth. On the reverse side the paint is denuded, but to a smaller extent.

XII Silvery: view of inner smooth surface of a flat valve, showing the almost complete absence of paint, a good spatting of Balanus, and a nest of tubicolous polychætes around the large hole. The reverse side is similar, but more paint remains in the roughened hollows.

The T-shaped black object between shells X and XI consists of a horizontal piece of tarred rope on which is growing a large mass of Botryllus and a little Leucosolenia.

Table XIII. Experiment G.

Observations on Growths (and Condition of Paint) on Untreated Shells and Shells Treated with Various Substances (I to VI, and VIII to XII, see p. 376) and put in the Sea on August 28th, 1919, at the West Wharf, Millbay Docks, Plymouth.

	Sept. 25, 1919 (exposed 4 weeks).	Dec. 8, 1919 (exposed 14½ weeks).	Feb. 7, 1920 (exposed *c.* 6 months).	May 19, 1920 (exposed *c.* 9½ months (see notes 1–3 below)
I Reddish brown anti-fouling	No growth	No growths; paint good, chipping a little on smooth faces	No growth; paint eroding	Paint entire on some shells, slightly washed off on others Balanus spat on bare shell and a few also on paint
II Green anti-fouling	No growth	No growth; paint good	No growth; paint slimy but still good coat	Paint mostly entire, slight growth only on naked shell
III Black anti-corrosive	Halichondria and a Polyzoan on 2 shells, other shells no growth	Heavy growth on all shells but one; paint in good to very good condition (see Table XIV)	Covered with Diplosoma, Botryllus, Halichondria mainly	Covered with growths, paint not examined
IV Reddish brown anti-fouling	No growth	No growth; paint good	No growth	Paint eroding, but still entire on some shells. A few Balanus spat actually on the paint. No growth on one shell
V Black-bronze anti-corrosive	Three shells with a little growth of Halichondria and young organisms	All but two shells with little to much growth (see Table XIV): paint good on most shells	Some shells without growth, paint not reported on	Shells covered with growth of various kinds: paint good
VI Reddish brown anti-fouling	No growth	No growth, paint already eroding easily	No growth; paint spongy; nearly all off on some sides	Paint good on a few shells, but is mostly badly eroded. A few Balanus on paint as well as on naked shell
VII Greyish white untreated shells	Three shells without growth. Halichondria, Hydroids, Botryllus, Hymeniacidon juv., and Amphipod nests, Diplosoma juv., on the others	Growth on all shells but one (see Table XIV)	Some shells now devoid of growth	All shells covered with good growths mainly of Botryllus, Balanus, and Diplosoma
VIII Red anti-corrosive	No growth, paint already sticky	Much Diplosoma on one shell, others no growth, but paint eroding fast	One shell covered with Diplosoma, others with paint spongy and eroding fast	Some shells still covered with paint but washed off others. Spat chiefly of Balanus is now established on the paint also (see note 4 below)
IX Black (varnish) experimental	Seven shells covered with growth of Halichondria, Hymeniacidon, Botryllus, Pomatoceros, Hydroids, and Amphipod (?) nests	All shells with growth: paint good on most shells (see Table XIV)	Some shells now without growth: paint good	All shells covered with growth: paint good
X Black coal-tar experimental	Four shells with growth of Halichondria, Ascidiella spat, and other unknown spat	Six shells with, 4 without growth: paint good on most shells (see Table XIV)	Good growth on shells	All shells covered with growth: paint good
XI Green anti-fouling	No growth	No growth; paint eroding easily	No growth; paint washing off	Some shells with paint entire but with little to much growth, chiefly of Balanus, on the paint as well as on the bare shell
XII Aluminium paint Silvery and experimental	No growth	Growth on 6 shells, but paint nearly all washed off all	Not observed	No paint or only a trace left. All shells covered with growth

1. August 16th, 1920. (Exposed about 12 months.) All the shells were restrung with tarred twine in the hope of further extended observations. On this date all the shells were found to be overgrown with marine animals of different kinds except the reds IV and I and the green No. II. In the case of No. II the paint was washed off most of the shells to some extent, and growths were found on the naked shell, but not on the paint.

2. September 30th, 1920. (Exposed about 13 months.) IV Red: Paint still good in parts on the rough side of the shell, there was little other growth than a few Balanus on the paint, but much on the denuded parts of the shell. II Green: Paint only good on the rough side of the shell where there is no growth: fair growth on those parts of the smooth side where paint is now washed off. Only 6 and 8 row sets of shells remained, the others having been lost.

3. April 23rd, 1921. (Exposed about 19 months.) Three shells of each of the paints I, II, and IV were collected and sent to the Government Chemist for chemical analysis of the parts. Only slight growth present on the paint, but shells otherwise with abundant growth.

4. Balanus spat have bored through the red oxide which is being pushed up on to the sides of the shell as the shell grows. The same phenomenon occurs when Balanus settles on red oxide on the bottoms of ships, and especially on surfaces covered with coal-tar, pitch, or varnish.

The Growth on Individual Shells in Experiment G on December 8th, 1919. (After 14½ Weeks in the Sea.)

The growths found on the individual shells in experiment G on December 8th, 1919, (i.e. after 14½ weeks' exposure in the sea), treated with substances III, V, IX, X, and the untreated shells (VII) are conveniently shown in Table XIV, below. It is noteworthy that the condition of the paints III, V, IX, and X, which are all black, was at this time very good; only occasional flaking occurred on the smoother side of the shells. The growths found on the painted shells therefore occurred actually on the paint and not on parts of the shell denuded of paint, as was the case, for example, with No. XII shells on this date and others later.

Table XIV.

Growths found on December 8th, 1919, (after 14½ Weeks in the Sea), on the separate Shells Treated with Substances III, V, IX, and X, and the Untreated Shells in Experiment G, West Wharf, Millbay Docks, Plymouth.

	VII	III	V	IX	X
No. of shell.	Untreated shells.	Black anti-corrosive.	Black-bronze anti-corrosive.	Black varnish experimental.	Black coal-tar experimental.
1	Halichondria 4 colonies	Botryllus	None	Diplosoma	Diplosoma abundant
2	Ascidiella young	Diplosoma Botryllus	Polydora	Halichondria	Halichondria 5 colonies Diplosoma
3	Halichondria Diplosoma Umbonula	Diplosoma Ascidiella young	Diplosoma Ascidiella young	Diplosoma Halichondria	None
4	Hydroids	Diplosoma	Diplosoma	Halichondria	Diplosoma Ascidiella juv. Polydora
5	Halichondria Botryllus Diplosoma	Diplosoma Pomatoceros Anomia	Halichondria	Halichondria 5 colonies	Diplosoma Polydora
6	None, dirty	Ascidiella Polydora Umbonula Anomia	Ascidiella young	Hydroids	None
7	Diplosoma Anomia Umbonula	None	Diplosoma Ascidiella young	Diplosoma	Diplosoma Botryllus
8	Botryllus	Anomia	None	Pomatoceros young	None
9	Botryllus Diplosoma	Botryllus Diplosoma Halichondria Hydroids	Diplosoma abundant	Pomatoceros Halichondria	Diplosoma Botryllus Halichondria a little
10	Diplosoma a little	None	Anomia Nudibranch spawn	Botryllus Diplosoma Halichondria Polydora	None

Summary of Results from Experiment G.

The most important results obtained from Experiment G are (1) the capacity of the different substances tested for resisting or permitting growth in the first few months of exposure in sea-water, and (2) the capacity of the different substances tested for resisting erosion from—or adhering to—rough and smooth surfaces.

The observations made on December 8th, 1919, and recorded in Table XIV, show that all the black paints, i.e. III, V, IX, and X, while remaining in good condition, permitted extensive growth to occur, while the observations made on September 25th, 1919 (see Table XIII), show that even in four weeks the same substances already had slight growths on them of the same kind as occurred on the untreated shells (VII) at that time. These substances must, therefore, be regarded as non-toxic, or at the most only slightly toxic, to the kinds of organisms shown in Table XIV. After nine months' exposure in the sea these paints remained in good condition and adhered to the shells better than the other paints, and were not again reported on. These paints need not be further considered in this experiment.

After 14½ weeks in the sea, paints VI, VIII, XI, and XII were found to be eroding fast, while I, II, and IV remained mostly in good condition, except for slight flaking on the smoother faces of the shell. At this time growths occurred on VIII and XII, but as the paint was already nearly all washed off the latter (XII), growth may have begun originally on the denuded parts of the shell. No. XII paint, therefore, was eroded in so short a period as 14½ weeks in this experiment and need not be further considered, except that it could be regarded as preventing marine growths for one month (see Table XIII).

After 6 *months in the sea* the following paints remain to be considered, namely I, II, IV, VI, VIII, and XI. Of these No. VI was spongy and washed almost completely off some of the shell-faces ; Nos. VIII and XI were soft and also being rapidly eroded ; the other paints remained good, but No. I was washing away to some extent.

After 9 *months in the sea* the paints VI, VIII, and XI were washed off most shells, and even where they remained permitted growths of Balanus. Nos. IV and I were also washing off to some extent and permitted Balanus to settle on the paint. No. II remained in the best condition, being washed off the shell in small areas in a few cases. In some of such cases growth had occurred on the denuded shell area.

After 12 *months in the sea* all shells were covered with growths except those painted with Nos. IV, I, and II ; of these Nos. IV and I permitted growths of Balanus on the paint itself, but no growth occurred actually

on No. II paint, although occurring on clean denuded areas of shell adjacent to the paint.

After 13 *months in the sea* the condition was almost the same as after 12 months. The paints II and IV still adhered well to the rougher faces of the shell, but was more or less washed off the smoother faces. No. IV still only permitted the growth of a few Balanus, while No. II still inhibited all kinds of growth, although not preventing such on adjacent clean shell area. No. I paint was not reported on on this examination.

After 19 *months in the sea*, shells, still covered with the paints IV, I, and II, and permitting little or no growth, were taken out of the sea and sent immediately to the Government Chemist for separate chemical analyses of the paints at this stage.

The results of this experiment confirm those in Experiment D especially, in which the paints were found to wash off the smooth side of the shells to a great extent in about 13–14 months. This period is not long enough to test fully the anti-fouling value of the more efficient kinds of poisonous paints, e.g. II, IV, and I, but serves to demonstrate the fundamental importance of the capacity of a paint of this kind (*a*) to withstand erosion and (*b*) to adhere to the surface to which it is applied. This and the other experiments with shells fully prove that all the paints adhere better to, and erode less quickly from, a rough than a smooth surface. In this experiment the anti-fouling paint VI eroded more quickly than VIII, and was, therefore, of less value for keeping down growth from this fact alone, whatever poisonous properties that paint may have had before erosion. It is obvious that an anti-fouling paint has lost its value as such as soon as it is washed away, therefore *the degree to which an anti-fouling paint resists erosion while retaining its growth-inhibiting properties is a fundamental property of such paints.*

SERIES III. PROMENADE PIER, PLYMOUTH.

Experiment H.

In this experiment the following substances only were tested, namely IV, anti-fouling paint; VIII, red oxide of iron paint; IX, black varnish; XV, a common grey paint; along with VII, untreated shells; XIII, sheets of copper 4 inches square; and XIV, sheets of zinc of the same size. The tarred rope (tarred with coal-tar and well dried) provided an additional experiment with No. X substance. The shells were painted with each paint, in lots of sixteen, and strung on tarred rope around the piles of the Promenade Pier at the level of low-water spring tides. Twenty shells were put out around each pile in two horizontal rows each containing ten shells, and in such a way that a clean shell alternated

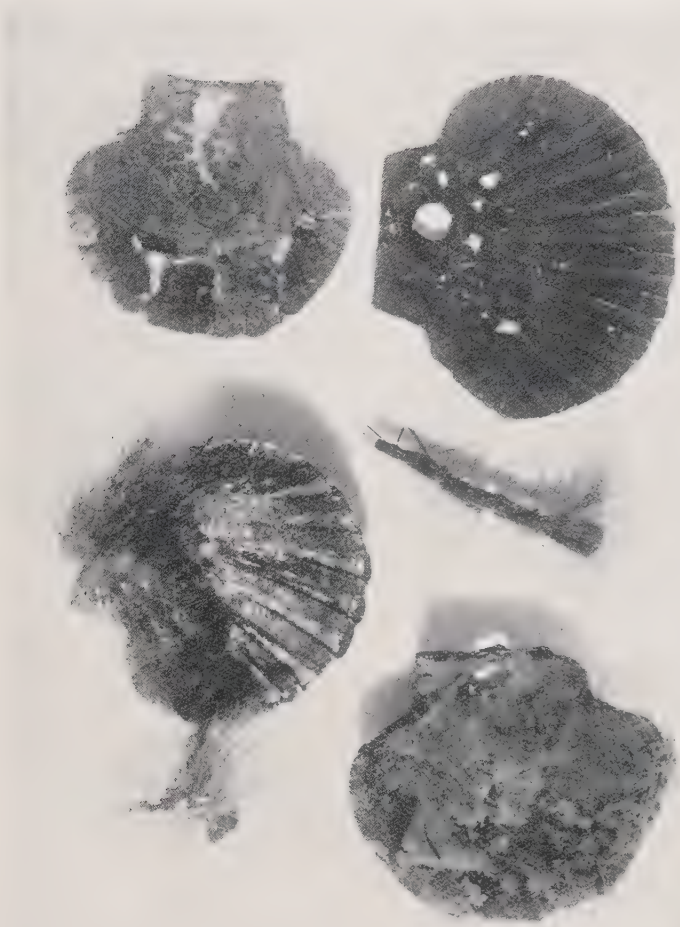


FIG. 17.—Photo of shells from Experiment H, Promenade Pier, Plymouth, exposed in the sea from June 18th, 1919, to September 13th, 1919. (× ca. $\frac{2}{5}$.) (Photo by D. P. Wilson.)

VII Untreated shell covered with a growth of six or seven distinct colonies of Botryllus, and with a slight growth of hydroids.

VIII Red: view of smooth inner surface of shell showing the paint washed off to a great extent and with mature Plumularia and Clytia overgrowing both the paint and the denuded shell. The reverse surface showed denudation of paint to a smaller extent, but hydroid growth both on paint and naked shell. The tarred rope still attached to this shell showed a luxuriant growth of Halichondria, Diplosoma, and ripe Plumularia.

IV Red: view of smooth inner surface of a flat valve, showing only slight loss of paint and no growth; the reverse side showed no loss of paint and no growth.

IX Black: view of smooth inner surface of a convex valve covered with colonies of Botryllus overgrowing the paint and ripe Plumularia and Clytia. The reverse side showed slight loss of paint on the ridges and similar luxuriant growth.

The piece of tarred rope between IX and X shells shows also a heavy growth of ripe Plumularia.

with a treated shell (with rare exceptions) both vertically and horizontally. Untreated shells alternating with the metal sheets were put out on piles not used for painted shells. The painted and untreated control shells were put out on June 18th, 1919, and the untreated shells and sheets of metal on June 20th, 1919. In this experiment the substances VIII, IX, and XV were only painted on the shells in one coat, but substance IV was given two coats. In all the other experiments two coats of each substance were applied. The shells were suitably marked by borings differing in size and position for identification. (See Fig. 6, p. 385.)

Observations on Growths and Paints in Experiment H.

After $5\frac{1}{2}$ *weeks in the sea*, on July 26th, 1919, it was found that the untreated shells had acquired either a little or a good growth mainly of Diplosoma (which yielded living active tadpoles in the Laboratory), Halichrondria, Plumularia (ca. half-grown colonies in abundance), and some Mytilus spat. Shells with No. IX substance and the tarred rope, X, had growths as luxuriant as on the clean shells.

IV was clean, in good condition, and without growth, except in three or four shells which showed slight growth (doubtless on parts of the shells denuded of paint, see later reports).

On XV the paint was washing away rapidly and already carried growths. XIII and XIV showed no growth.

On the pile to which the shells were attached was an abundant growth of *Halichondria panicea* which rapidly overgrew the tarred rope and crept on to the clean shells. Creeping growths of this kind were observed *on this day* to have been undoubtedly arrested on reaching both the paint No. IV and the zinc sheets No. XIV.

After 8 *weeks in the sea*, on August 12th, 1919, VII, IX, and X all showed good growths of little to luxuriant Diplosoma, Halichondria (one colony $3{\cdot}2\times2\times1$ cms.), *Plumularia pinnata* and *setacea* (both of which extruded planulæ), Clytia (which yielded medusæ), Botryllus (one colony with fifteen whole and three half-systems), and other hydroids. XIII showed no growth, but of XIV (zinc) one sheet had a small colony 10×3 mm. of Halichondria which had almost certainly grown from a larva.

XV had fair growths and VIII a little growth on two shells, but none visible on others.

After $12\frac{1}{2}$ *weeks in the sea* (see Fig. 17, p. 419), on September 13th, 1919, a detailed report on the shells was made which may be summarised as follows :—

VII, untreated shells : four shells with little growth, others (ca. 70) mostly covered with growths of Botryllus, Diplosoma, Plumularia, Clytia,

Bougainvillea, and other hydroids. One shell placed between two sheets of copper had no visible growth on this day.

IV, reddish brown anti-fouling paint. All shells without growth and the paint in good condition and entire on nearly all the shells.

VIII, red oxide ; the paint is washed off the inside (smooth face) of most shells. Five shells with no growth, others with small growth of hydroids, others with young colonies of a compound Ascidian (probably Morchellium) and Botryllus and Diplosoma overgrowing the paint.

IX, black varnish shells covered with same growth as on others, and paint still good.

X, tarred rope with luxuriant growths and overgrowths.

XIII, copper sheets ; all without growth.

XIV, zinc sheets ; thirteen no growth, two with slight hydroid growth. one with a small colony of Halichondria now 12×5 mm.

XV, the grey paint is almost all washed away on all shells, which have now acquired little to luxuriant growths. On this day tadpoles of Botryllus and Diplosoma were obtained from samples of the growth on the material, and medusæ of Clytia from isolated colonies. On September 15th numerous *Folliculina ampullaria* were obtained in a bowl from material isolated September 13th. This species had passed through a reproductive phase in the Laboratory. On October 24th three sets of shells were missing. *Bougainvillea ramosa* collected from the experimental material gave off medusæ.

After 25 *weeks in the sea*, on December 9th, 1919, the shells, No. IV, showed no growth, but the paint was washing off badly on the smoother side of the shells. Bougainvillea colonies and Sycon were now abundant on most of the other material, in addition to the organisms already recorded.

After $8\frac{1}{2}$ *months in the sea* all the No. IV shells had lost a large amount of paint ; one shell had no paint at all left. There was, however, no growth on the residual paint itself.

Many of the untreated shells, No. VII, were being washed clean by the wave-action resulting from heavy gales ; colonies of Botryllus were found just hanging on to the shells.

On February 21st, 1920, the shells were restrung with fresh rope or trawl twine.

On August 18th, 1920, many strings of shells were missing. Four sheets of copper were found to be very thin, but there occurred a luxuriant growth of organisms all around the copper sheets which obviously have no effect on keeping down growth to within a distance of even a few millimetres. There was, however, no growth on the copper itself.

On this day Halichondria from the shells yielded embryos. No further observations were made.

Table XV.

Summary of Results from all Experiments, showing incidence of Growths* and Final Condition of the Substances Tested.

Experiment / Observations	Cawsand Bay				West Wharf			Prom. Pier	
	A and B on wood	C on wood	D and E on shells smooth surface	D and E on shells rough surface	F§ on wood	G on shells smooth surface	G on shells rough surface	H on shells smooth surface	H on shells rough surface
I Growth	little	fair amount	*abundant*	*abundant*	little	little	little	—	—
in period	14 months	14 months	14 months	14 months	12 to 28 months	9½ months	9½ months		
paint	nearly done	some†	trace	trace	fair amount	eroding slightly	eroding slightly		
in period	14 months	14 months	14 months	14 months	28 months	9½ months	9½ months		
					trace 42½ months				
II Growth	trace	little	*abundant*	none	none	none	none	—	—
in period	14 months	14 months	14 months	14 months	28 months	13 months	13 months		
paint	entire	some	trace	partly washed away	fair amount	much eroded	slightly eroded		
in period	14 months	14 months	14 months	14 months	42½ months	13 months	13 months		
III Growth	fair amount	abundant	abundant	abundant	abundant	slight	slight	—	—
in period	6 weeks	6 weeks	from 6 weeks	6 weeks	from 6–9 months	4 weeks	4 weeks		
paint	good	some	partly washed off	entire	good where not	not recorded	not recorded		
in period	14 months	14 months	14 months	14 months	eaten, 42½ mths.	13 months	13 months		
IV Growth	little	little	fair amount and	none to little	little	little	little	none	none
in period	14 months	14 months	*abundant*	14 months	12–20 months	13 months	13 months	8½ months	8½ months
			14 months						
paint	fairly good	some	partly washed off	almost entire	fair amount	badly eroded	slightly eroded	badly eroded	badly eroded
in period	14 months	14 months	14 months	14 months	42½ months	13 months	13 months	6 to 8½ months	9 months
V Growth	fair amount	abundant	abundant	abundant	slight	little to much	little to much	—	—
in period	6 weeks	6 weeks	from 6 weeks	from 6 weeks	from one month	4 to 14½ weeks	4 to 14½ weeks		
paint	good	some	little to ½ eroded	almost entire	eaten away	good	good		
in period	14 months	14 months	14 months	14 months	20–28 months	9½ months	9½ months		
VI Growth	slight	much	slight	abundant	abundant	slight	slight	—	—
in period	6 weeks	14 months	9 weeks	14 months	6–9 months	9½ months	9½ months		
paint	little left	some	almost all eroded	trace to ½ eroded	eroding in 12	eroded	mostly eroded		
in period	14 months	14 months	14 months	14 months	none left	6–9 months	9 months		
					28–31 months				
VII Growth	fair amount	abundant	abundant	abundant	almost eaten away	abundant	abundant	fair amount	fair amount
in period	6 weeks	6 weeks	6 weeks	6 weeks	20 months	4–14½ weeks	4–14½ weeks	5½ weeks	5½ weeks

VIII	Growth in period	fair amount 6 weeks	abundant 6 weeks	fair amount from 6 weeks	fair amount from 6 weeks	abundant 1 to 2¾ months	slight 3½ to 6 months	slight 3½ to 6 months	fair amount 12½ weeks	fair amount 12½ weeks
	paint in period	little left 14 months	some 14 months	trace 14 months	trace 14 months	eroded or eaten 12–20 months	mostly eroded 3½ to 6 months	eroding badly 9 months	badly eroded 12½ weeks	somewhat eroded 12½ weeks
IX	Growth in period	—	—	—	—	fair amount one month	much one month	much one month	fair amount 5½ weeks	fair amount 5½ weeks
	paint in period					almost entire 28 months	good 9½ months	good 9½ months	good 25 weeks	good 25 weeks
X	Growth in period	—	—	—	—	abundant 2¾ to 6 months	fair amount one month	fair amount one month	—	fair amount‡ 5½ weeks
	paint in period					almost entire 28 months : good where not eaten 42½ months	slightly eroded 3½ to 9 months	good 9 months		good 8 months
XI	Growth in period	—	—	—	—	*abundant* 9–12 months	slight 9 months	slight 9 months	—	—
	paint in period					washed away 12 months	badly eroded 3½ to 9 months	eroded badly 9 months		
XII	Growth in period	—	—	—	—	abundant 9–12 months	slight 14½ weeks	slight 14½ weeks	—	—
	paint in period					entirely eroded 20–28 months	badly eroded 14½ weeks.	badly eroded 14½ weeks		
XV	Growth in period	—	—	—	—	—	—	—	slight 5½ weeks	slight 5½ weeks
	paint in period								badly eroded 5½ to 12½ weeks	badly eroded 5½ to 12½ weeks

XIII and XIV XIII acquired no growth but became thin in 14 months
XIV acquired a slight growth in 8 weeks on one sheet only and on 3 sheets in 12½ weeks.

* If the records of growth are given in italics, they refer to growth on the shell or surface denuded of paint; otherwise they refer to growth on the paint.
† The condition of the paint in this experiment after 14 months' exposure could not be determined accurately owing to bad weather, but it was easily seen that all the boards had some paint remaining.
‡ In this experiment No. X, coal-tar, was only tested on tarred rope, which must be regarded as having a rough surface.
§ The erosive influences operating in this experiment (F) must be considered : (1) water erosion, (2) attrition of the paint by gribble either by ingestion or undermining the underlying wood, and (3) possibly also unusual chemical action with the substances involved in typical dock-side water-pollution.

Results of Experiment H.

It was found that the anti-fouling paint No. IV resisted growths so long as the paint remained on the shells, that is, during $8\frac{1}{2}$ months only, in this experiment. This paint washed off the smoother faces of the shells much more rapidly than the rough face.

No. XIII, sheet copper, resisted growths so long as observed, i.e. ca. 14 months, but did not prevent marine growths occurring within even a few millimetres' distance.

No. XIV, sheet zinc,* inhibited growth for only a short period; after only 8 to $12\frac{1}{2}$ weeks in the sea a small proportion of the sheets used acquired a slight growth of Halichondria or hydroids.

No. IX, black varnish, became overgrown as soon as, and as much as, untreated shells, but remained in good condition longer than the other paints.

No. X, coal-tar on the rope, acquired growth as soon as, and apparently more profuse than, the clean shells.

No. XV, an ordinary grey paint, became washed off the shells to a great extent in only $5\frac{1}{2}$ weeks and had disappeared after $12\frac{1}{2}$ weeks.

No. VIII, red oxide, inhibited growth during 8 weeks so long as it remained on the shells. This paint was washed off the smoother faces of the shells more rapidly (ca. $12\frac{1}{2}$ weeks) than off the rougher faces, and began to be overgrown (where it still adhered) after $12\frac{1}{2}$ weeks.

In this situation erosion was more rapid than in corresponding experiments at the West Wharf and Cawsand Bay.

Experiment J.

This experiment has previously been partially recorded (**1**, 1914), but is included here briefly for comparison with others. The Cawsand Bay raft (see p. 380) was moored in the sea after being well coated with coal-tar on March 12th, 1912. Thirty-one weeks later, on October 15th, 1912, the raft was brought in and beached above high-water mark. Living *Teredo norvegicus* (not *navalis* as previously recorded) were taken from the boards of the raft on October 15th, and a re-examination was made for others on October 31st and November 2nd after the raft had been a fortnight out of water. On November 2nd four large individuals were taken out of the wood and one was found to have cilia on the gill beating quite actively; the other three had recently died.

The largest specimen measured, fresh out of its burrow, was 19·8 cm. long. The largest boring was 28 cm. long, and had a mean diameter of

* Zinc-coated buoys acquire a heavy growth of many kinds of organisms after only a relatively short period in the sea, namely, one to two years. The zinc, however, becomes coated with a white substance, probably a zinc salt which has not been investigated and is apparently non-toxic or only slightly toxic.

about 1 cm. (see Fig. 18, below). The raft was made of common wood and was presumably pine. The general growth on the raft during 1912 was similar to that recorded in 1919 (see p. 396), and similar growth has been repeated during many seasons, therefore there is no doubt that coal-tar is of no value whatever for preventing marine growths or for preserving wood from the attacks of Teredo. On the other hand, Experiment G proves that coal-tar is a valuable agent for preserving wood from the attacks of gribble, i.e. *Limnoria lignorum* and *Chelura terebrans*, in English waters.

Experiment K.

A number of bathing rafts (usually three, sometimes four) are put out in the sea each year off Plymouth Hoe about the end of April and taken in again about the middle of the following October. It has been possible to make observations on these rafts over a number of years, owing to the courtesy of Mr. A. L. Bennetts of the Plymouth Corporation. The bottoms of these rafts are either well coated with two good coats of coal-tar or are thickly covered with pitch. Growth occurs quickly and luxuriantly on the bottoms and on the sides, comparable with that obtained on the Cawsand Bay raft; for example, Mytilus settles on the bottom and grows *in situ* each year to a size of

FIG. 18.—Photo of a piece of wood carved to expose two large Teredo borings from Experiment J, Cawsand Bay Raft, after 31 weeks' immersion in the sea. (× ca. $\frac{2}{5}$.) (Photo by D. P. Wilson.)

A. The point of entry of one Teredo which bored to the middle of the wood and then continued its course in the middle. The end of the boring is not quite exposed.

B. The point of entry of another Teredo which, in order to avoid a nail, bored at first towards the side and then turned inwards, but found itself approaching the wetter and more external wood; whereupon it abandoned the last part of the burrow, sealed it with a calcareous partition from the main burrow, and changed direction completely to bore down the middle. The end of the burrow is not lined with calcareous matter and is not completely exposed.

3 to 4 cm. approximately; and in 1914 mature *Ciona intestinalis* grew up to 10·5 cm. long, mature *Ascidiella aspersa* up to 5·9 cm., *Sycon coronatum* to 8·2 cm. long, carrying embryos; and other growths occurred comparable in general to that obtained on the Cawsand Bay raft (see p. 396). It is clear therefore that coal-tar and pitch are not deterrents to growth *in the sea*, and indeed when well-dried favour growth by offering at once a clean non-toxic surface for the organisms.

Summary of Results from all Experiments.

The results obtained in all the experiments are collected together in Table XV, p. 422, and can now be considered. Experiments may be

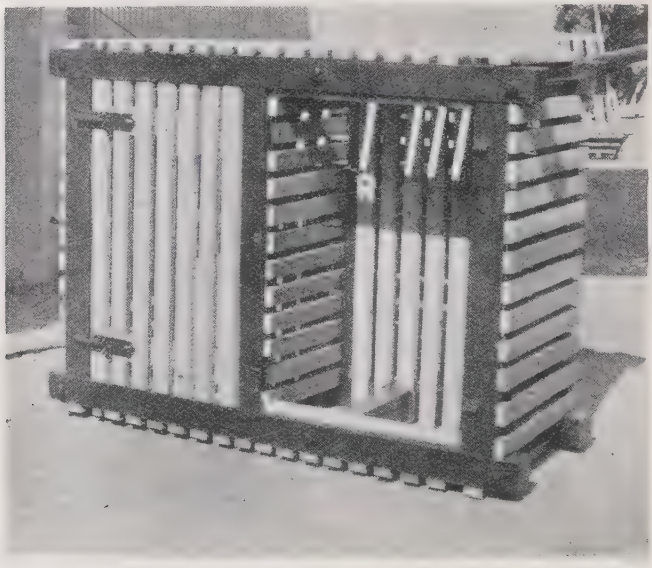


Fig. 19.—Photo of an upper view of a raft similar to, but three times as small as, the one used in Cawsand Bay.

One lid has been removed to show the internal structure. Every piece of wood can be removed for observation of growth and can be replaced by a new piece without interfering with the structural basis of the raft. See Fig. 20 for under-surface view. This raft was used for experiments on rate of growth at Spitzbergen in 1921 (**30**). (Photo by A. J. Smith.)

referred to conveniently by letter to save repetition of the word "experiment."

It is clear from Table XV that the only paints having effective anti-fouling values are I, II, and IV. It is also manifest that the anti-fouling value depends upon the retention of the paint on a substratum (see especially the series of experiments on paints Nos. II, I, and XI).

All the paints are retained better on wood than on shells (compare F and G) and better on the rougher face of the shells than on the smooth

face (see D and E, G and H). On wood the paint was eroded less quickly in a situation subject to less erosion, as in F, than in one subject to greater erosive influence as in A, B and C (compare also Table I, p. 382, and Table IX, p. 402, especially with regard to No. I paint). On shells there is an indication that erosion occurred roughly in proportion to the erosive effect of the sea-water in the different situations. Compare G in a relatively quiet situation with D and E where motion was continuous.

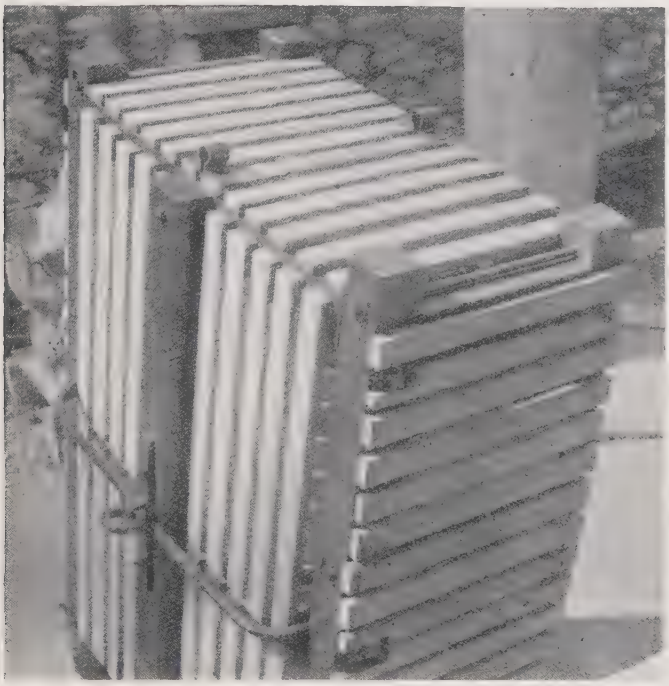


FIG. 20.—Photo of a raft similar to, but much smaller than, the one used in Cawsand Bay to show the under surface and side construction.

The bar of iron with loop for the swivelled shackle of the mooring-chain is also looped around the middle of each of the stout side-pieces which form a part of the basic skeletal structure of the raft. See also Fig. 19. The bolting of the basic parts is also shown. (Photo by A. J. Smith.)

In H, however, No. IV paint eroded badly on the rougher face of the shells in 9 months, but it is possible that in this situation wave action at about the time of low water is exceptionally severe in winter, while it is probable that some rubbing occurred as well as water erosion.

It is significant that the proprietary anti-fouling paints VI and XI eroded rapidly and also permitted growth early, even when not eroded. See especially A and B, VI, for growth ; and F, XI, for erosion.

The anti-corrosive substances III, V, and VIII all permit early growths,

but while the latter eroded rapidly both on wood and shells the two former adhered to shells (and would presumably also adhere to iron) better than the best anti-fouling paint. On wood, however, No. V was rapidly eroded probably partly by gribble, whereas No. III remained in good condition and preserved the wood as long as any of the anti-fouling paints except No. II.

In its property of preserving wood (and probably also iron) coal-tar No. X was as efficient as the proprietary paint No. III, and more efficient than No. V, while so far as the observations were continued black varnish No. IX was shown to be equal in value as a preservative on wood to No. III and better than V.

Common paints such as XII and XV were shown to be rapidly eroded and to have only a slight preservative and anti-fouling value. Zinc, it was shown, might soon lose its toxic effect in the sea, but copper retained its anti-fouling property during the period of the experiment, but dissolved somewhat rapidly in the sea-water.

The most critical situation from an anti-fouling point of view is where a strong light plays on the paint, for No. II paint, which remained free from growth during at least 28 months in Experiment F, acquired some algal growth in 7 to 14 months in Experiment C.

LIMITATIONS OF THE EXPERIMENTS.

In order to compare the results obtained from the experiments herein recorded with those likely to be obtained in actual practice, i.e. on the bottoms of ships or other structures, it is necessary to compare the conditions under which the experiments were carried out with those occurring in actual practice.

The Nature of the Surface covered by the Experimental Substance.

In practice, iron ships, after being scraped and cleaned, are usually painted first with red oxide paint (such as No. VIII in the experiments), which is used as an (iron) anti-corrosive agent. When this coat is dry it is painted over sometimes with one or two coats of quick-drying anti-fouling paint, such as Nos. I, II, IV, VI, and XI in the foregoing experiments. Wooden ships after being scraped and cleaned—and more or less dried—are painted with the anti-fouling paint at once.

In the experiments the test-boards and shells were painted with two coats of anti-fouling paint, which were well dried on the same day or the day before the material was put in the sea. The treatment in the experiments with regard to painting is therefore comparable to, but better than, that given to iron vessels. With iron vessels the anti-fouling paint is usually directly applied on red oxide; and it is possible, and indeed

probable, that the behaviour of the anti-fouling paints in the sea differs according to the nature of the underlying surface. In this respect there are three conditions to be considered, namely :—

(*a*) Anti-fouling paint on iron oxide over iron.
(*b*) Anti-fouling paint directly painted on to wood.
(*c*) Anti-fouling paint directly painted on to shells.

Experiments A, B, C, and F are of the (*b*) type and the remaining experiments of the (*c*) type. No experiments of the (*a*) type were tried.

Conditions Conducive to Erosion.

The paint on the bottom of a ship is subjected to erosive effects in proportion to the speed of the ship and the period of time the boat is in motion. In Experiments A to E the experimental material was in effect buoyed and would be subject to almost continuous motion by the lifting motion of the waves as well as the slight pitch and roll of the buoy (i.e. the parallelopiped-shaped raft, $20 \times 5 \times 2$ feet). In Experiment F the test-boards were fixed and experienced no subjective motion. In Experiments G and H the material was also fixed with tarred rope, but in these cases the shells were liable to be, and were in instances, worked loose by wave action.

In Experiments A to E in Cawsand Bay the experimental material would be liable to erosion by slight tidal currents, and H at the Promenade Pier by similar tidal currents and wave action, especially at low water, while F and G at the West Wharf would only experience slight erosion due to the rise and fall of the tide and that due to slight wave action (in this protected situation) at low water.

Experiments A to E were therefore subject to relatively great erosive influences, but probably not so great as that experienced by even a 10-knot vessel ; the painted surfaces in the other experiments would experience proportionately milder erosive action.

Condition and Dryness of the Surfaces Painted.

The surface of the bottom of an iron vessel which has been cleaned and scraped will vary from smooth to roughly pitted according to the number of times the bottom has been scraped and the degree of fouling experienced. The surface of the bottom of a wooden vessel will vary in a similar way, but will become more uneven than that of an iron ship.

In Experiments A, B, C, and F the wood was glass-papered to a smooth but not polished surface ; and in the shell experiments the inner face of each shell is of a polished smoothness, while the outer face is roughened with fine decussations, except in some of the convex valves which might be smooth-worn on the crown of the shell.

In all the experiments the experimental material was in a dry condition when painted, whereas when ships are painted under economic conditions the bottom is liable to be wet or damp in rainy or damp weather, or when docking is carried out hastily.

Thus on the whole the experimental paints would be applied more efficiently than under economic conditions, and to a variety of surfaces roughly comparable to those occurring on the bottoms of ships, but would be subject to less water erosion than on even slow-moving vessels (say, 10 knots) if such vessels are in fairly continuous translation.

PART II. CHEMICAL INVESTIGATIONS.

During the course of these experiments and observations the question arose during the concurrent investigation by the writer of the cause of unusual oyster mortality (**14** and **15**, 1921, 1923–24) as to what order of concentration of arsenic and copper particularly was likely to be poisonous to oysters and other marine animals. Fortunately, samples of paints which had been in the sea a considerable time while remaining poisonous were still available from the experiments herein described.

As it was possible to derive valuable information regarding the resistance of marine animals to poisons from chemical analyses of paints which (*a*) retained their poisonous properties in the sea and (*b*) were just losing their poisonous properties and beginning to be overgrown, the assistance of the Government Chemist was asked for and happily obtained for making a few critical analyses.

It is necessary to point out that a thorough chemical and biological study of the question was not contemplated in this research. In order to study the problem in such a way it would be necessary to know all the chemical ingredients used in the manufacture of the paints, but as the chief substances tested were proprietary articles, which are of great economic value, it was manifestly impossible to obtain the information.

The chemical investigations in these experiments are therefore limited to :—

(1) The analyses of three anti-fouling paints after exposure to sea-water and retention of anti-fouling property for 19 months.

(2) The analyses of two of the same paints as in (1) after exposure to sea-water on test-boards for $42\frac{1}{2}$ months, when the paints had either lost, or were apparently just about to lose, toxicity to marine animals.

(3) The analyses of samples of two original paints (the same as in (2)) from the original paint-can.

These analyses were made in the Government Laboratory by the Government Chemist and his staff, to all of whom we are indebted for the resultant general information.

Analyses of three Paints which Retained Poisonous Properties after remaining 19 Months in the Sea.

Three of the shells used in Experiment G put out in the sea on August 28th, 1919, were collected from the West Wharf, Millbay Docks, Plymouth, on April 22nd, 1921, and forwarded the same day to the Government Chemist for chemical analysis of the paint remaining on the shells. At this time most of the paint on the smoother face of the shells had been washed away, but where the paint remained there was little growth other than Balanus in I and IV, but none on II, although good growth occurred on adjacent areas of the shell denuded of paint. (See notes to Table XIII, p. 415.)

Thus on this date paints I and IV were still toxic to most marine animals, and paint No. II was still poisonous. The Government Chemist reported (**15**, 1924, p. 41) that "The paints were scraped off with as little of the shell matter as possible and give the following results :—

Lab. No.	Paint.	Colour.	Lead.	Zinc. per cent.	Copper per cent.	Arsenic as As_4O_6 per cent.
32	IV	Red	Absent	0·95	5·79 (cuprous)	0·01
33	I	Red	Absent	0·85	7·91 (cuprous)	0·01
34	II	Green	Absent	0·04	16·56 (cupric)	2·60

No evidence of Mercury nor of Barium was obtained in any of the paints, but Nos. 32 and 33 contained large proportions of iron."

It is clear from these analyses that the paints I and IV are very much alike in constitution as in behaviour (see Table XV, p. 422) but contain very much less copper and arsenic than No. II. The combination of the metals zinc, copper, and arsenic in these paints with the respective percentages of approximately 1·0 zinc, 6 to 8 (cuprous) copper, and 0·01 per cent arsenic is one which is just approaching the limit of toxicity in seawater. This is a valuable result, even though the actual chemical constitution of the original materials is unknown.

The high percentage of cupric copper and arsenic remaining in paint II is sufficient explanation of the retained toxicity and a tribute to the efficiency of the matrix in this paint after 19 months' exposure on a shell surface in the sea.

Analyses of Paints on Test-Boards after about $3\frac{1}{2}$ Years in the Sea.

The paints II and IV on the test-boards used in Experiment F were analysed after remaining in the sea about $3\frac{1}{2}$ years. The condition of these two test-boards with regard to overgrowth is given in detail in the section beginning on p. 410, and is depicted in Fig. 12, p. 404, and Fig. 13, p. 405.

In the case of No. IV test-board, two areas of paint were scraped off and analysed. Both these areas had undoubtedly lost toxicity and were covered with living organisms when taken from the sea (see Fig. 12). The zinc-copper-arsenic percentage in these two samples of paint had been reduced greatly below that found to be near the limit of toxicity in the preceding sample, and had doubtless been non-toxic for some time, as may be also adjudged especially from the size of the barnacles (Balanus) which were growing on the analysed paint.

The condition with regard to overgrowths on the areas of paint, A to D, analysed from the front face of test-board II were as follows, but see also Fig. 12, p. 404.

	Site.	Region.	Growth.
Area A	Around the fixing nail 10 to 18·4 inches from the top.	In the upper middle region of the board.	Covered in part with a growth of the hydroid Obelia and with a few borings of gribble in a crack in the wood.
Area B	4·5 to 8·8 inches from	the bottom of the board	with 3 large and a few small borings of gribble, i.e. Limnoria or Chelura.
Area C	10·5 to 14·7 inches from	the bottom of the board, i.e. in the lower half.	No growth observable.
Area D	5·6 to 9·8 inches from	the top of the board.	No growth observable.

The bottom of the board was covered with a growth of Diplosoma, Umbonula, and Halichondria up to a height of 5 or 6 inches from the lower edge ; this growth probably encroached slightly on the lower part of area B, which was scraped for chemical analysis.

The results of the analyses of the samples of paints scraped from areas A to D are given in the following report by the Government Chemist with a discussion on the significance of the figures obtained, together with analyses of the original paints from the paint-can.

THE GOVERNMENT CHEMIST'S REPORT ON CHEMICAL ANALYSES.

"REPORT ON THE EXAMINATION OF TWO SAMPLES OF ANTIFOULING PAINT RECEIVED FROM DR. ORTON ON 15TH MARCH, 1923, AND OF THE PAINT REMAINING ON AREAS OF TWO WOODEN BOARDS TO WHICH THESE PAINTS HAD BEEN APPLIED WITH DIFFERING TOXIC EFFECTS AFTER $3\frac{1}{2}$ YEARS IMMERSION IN SEA-WATER.

The paints were described as :—

Lab. No. 323. 1. (Green paint)

Lab. No. 324. 2. (Brown paint)

and gave the following results on analysis :—

TABLE 1.

ANALYSES OF NO. II AND NO. IV ORIGINAL PAINTS.

	Green per cent.	(Reddish) brown per cent.
Volatile matter (turpentine substitute)	22·4	21·6
Oil	18·7	15·9
Oxidised oil and varnish gums	8·6	10·5
Silica and silicates	1·2	5·6
Lead oxide	0·1	nil
Arsenious oxide	5·0	0·2
Cupric oxide	14·8	*nil*
Cuprous oxide	*nil*	11·8
Iron oxide	0·4	15·4
Zinc oxide	0·8	0·5
Calcium oxide	8·6	9·3
Carbon dioxide	4·6	8·3
Phosphoric pentoxide	0·2	nil
Magnesium oxide	0·2	0·9
Sulphuric anhydride	8·6	nil
Acetic acid and a little undetermined organic matter (by difference)	5·8	nil
	100·0	100·0

In the green paint the copper appears to be present partly as insoluble basic sulphate (and some of the lime might also be linked up with this) and partly as aceto-arsenite of copper (Scheeles green). The calcium-oxide is in combination with the carbon dioxide and with part of the sulphuric anhydride. It is impossible to give the exact composition of such a mixture.

In the case of the brown paint the copper is present in the form of red cuprous oxide and the calcium and magnesium oxides are in combination with the carbon dioxide forming carbonates.

The paint on the boards was very thin and only small quantities were obtained from the areas scraped. There was not sufficient material, therefore, for complete analyses. The most important constituents have

been determined but the results are complicated by the fact that silicious material, carbonates, sodium salts, etc., have been deposited in the paint. Before scraping off the samples all organic growth was removed together with any incrustation that obviously did not belong to the paint. In the case of the brown board sample A was taken from a place competely overgrown, while the area sampled for B was fairly clean except for five or six barnacles.

Four areas of the green-painted board were marked A, B, C, and D by Dr. Orton, who stated that 'the part A has a growth of hydroids roughly within the circle,' and 'parts B, C, and D are apparently all just losing toxicity.'

The results of the analysis are as follows :—

TABLE 2.

ANALYSES OF PAINT SCRAPINGS FROM TEST-BOARDS II AND IV. EXPERIMENT F.

(*a*) *Green board* (II)

	Partly covered by a growth of hydroid. A %	Bored by gribble and slightly overgrown. B %	No growth. C %	No growth. D %
Insoluble in acid. Oxidised oil, wood and organic matter	14·1	14·5	12·1	14·4
Insoluble in acid. Mineral matter, silica and silicates	30·8	34·8	28·8	11·2
Cupric oxide	4·0	2·2	7·5	15·2
Iron oxide	4·5	6·3	5·0	2·4
Zinc oxide	0·2	0·3	0·4	0·2
Calcium oxide	22·6	30·4	11·2	8·5
Magnesium oxide	1·4	1·6	1·8	0·9
Arsenious oxide	0·4	trace	0·7	0·7
Phosphorous pentoxide	0·6	0·5	0·3	0·3
Undetermined—CO_2, chlorides, sulphates, moisture, soluble organic matter, and sodium salts	21·4	9·4	32·2	46·2
	100·0	100·0	100·0	100·0

(*b*) *Brown board* (IV)

	Overgrown with marine organisms and non-toxic. A %	B %
Insoluble in acid. Oxidised oil, wood and organic matter	17·5	16·5
Insoluble in acid. Mineral matter, silica and silicates	16·9	19·3
Cuprous oxide	0·2	0·6
Iron oxide	16·4	16·0
Zinc oxide	0·5	0·6
Calcium oxide	24·2	19·2
Magnesium oxide	2·6	2·2
Arsenious oxide	nil	0·05
Phosphorous pentoxide	0·4	0·3
Undetermined — CO_2, chlorides, sulphates, moisture, soluble organic matter and sodium salts	21·3	25·3
	100·0	100·0

It will be seen that in both sets of samples there are notable increases in the proportions of silicious material and calcium oxide while in the samples from the green board the iron has unaccountably increased.

In order to obtain a better comparison of the main inorganic constituents of the scrapings with those of the original paints the basic constituents (including silica and silicates and arsenic) have been added together and worked out on a 100 per cent basis. The figures are as follows :—

TABLE 3.

PERCENTAGE OF BASIC CONSTITUENTS (INCLUDING SILICA, SILICATES, AND ARSENIOUS OXIDE) IN THE ORIGINAL PAINTS II AND IV AND IN SAMPLES EXPOSED IN THE SEA FOR $3\frac{1}{2}$ YEARS.

(*a*) *Green board* (II)

	Original paint. %	Areas after $3\frac{1}{2}$ years exposure in the sea. With Hydroid growth. A %	With gribble borings. B %	No growth. C %	No growth. D %
Basic constituents (including silica and silicates)	31·1	63·9	75·5	55·4	39·0
Silica and silicates	3·9	48·2	46·1	52·1	28·7
Lead oxide	0·3	nil	nil	nil	nil
Arsenious oxide	16·1	0·6	tce.	1·2	1·7
Cupric oxide	47·5	6·3	2·9	13·5	39·0
Iron oxide	1·3	7·0	8·3	9·1	6·0
Zinc oxide	2·6	0·3	0·4	0·7	0·6
Calcium oxide	27·6	35·4	40·2	20·1	21·7
Magnesium oxide	0·7	2·2	2·1	3·3	2·3
	100·0	100·0	100·0	100·0	100·0

(*b*) *Brown board* (IV)

	Original paint. %	Overgrown area. A %	Overgrown area. B %
Basic constituents (including silica and silicates)	43·7	60·9	57·9
Silica and silicates	12·8	27·8	33·2
Arsenious oxide	0·5	nil	0·1
Cuprous oxide	27·0	0·4	1·0
Iron oxide	35·2	26·9	27·7
Zinc oxide	1·1	0·8	1·1
Calcium oxide	21·3	39·8	33·1
Magnesium oxide	2·1	4·3	3·8
	100·0	100·0	100·0

The results from the green (arsenic) board are peculiar. Sample B contained the largest proportion of basic constituents and silica, i.e. 75·5 per cent, the bulk of this consisting of silica and silicates and calcium oxide.* Since practically all the arsenic and most of the copper have been washed out, this paint should have lost its toxicity to a greater extent than A which still contains 0·6 and 6·3 per cent respectively of arsenious oxide and copper oxide. Samples C and D should be more toxic than A and it will be seen that whereas in A and B there is an increase in the proportion of calcium oxide which is presumably due to shells* of minute organisms, the proportion in C and D is less than in the original paint, pointing to the paint surface still being obnoxious to the organisms. The proportion of basic constituents and silica in D is only 39·0 per cent as compared with 63·9 per cent in A.

The apparent increase in the iron content of the scrapings may have been caused by deposition of rust or some insoluble iron deposit from the sea water, or it may be due to the ferric oxide in the original paint being very much more resistant to the sea water than all the other constituents of the paint.

In the case of the brown (copper) board it can be said that the cuprous oxide has been almost completely washed out and there is little difference in the copper content on the area completely overgrown (A) and on the area only partially overgrown (B).

It is, however, practically impossible from the limited number of results to trace the changes which have occurred in the paints during exposure. The composition of the paint is affected on the one hand by *removal* of constituents, organic and inorganic, and on the other by *addition* of inorganic matter in the form of calcium carbonate and silicious material derived either from the sea water or from organisms inseparable from the surface of the paint, or of organic matter, from the organisms or from the underlying wood, which could not be separated from the scraped paint.

The results of the analysis of the paints on three shells which were given in the oyster mortality investigation report of 14th July, 1921, in terms of metallic copper and zinc may be stated, for comparison in terms of the compounds found in the original paints as follows :—

Lab. No.	No. of paint.	Cuprous oxide. %	Cupric oxide. %	Zinc oxide. %	Arsenious oxide. %
32 (red)	IV	6·52	—	1·18	0·01
33 (red)	I	8·91	—	1·06	0·01
34 (green)	II	—	20·71	0·05	2·60

* The excess of calcium oxide in this sample was probably derived from the encrusting Polyzoan on the lower part of area B (see p. 432). J. H. O.

These results show that the brown paint on the shells had lost cuprous oxide, and the green paint had lost arsenic. The apparent increase of copper oxide in the green paint shows only that during its exposure to the sea the paint had lost less of its copper oxide than of other constituents. In illustration of the apparent increase it may be noted that if the original green paint had lost all its volatile matter and 3 per cent of arsenic, the remaining paint would contain 19·8 per cent of cupric oxide and 2·6 per cent of arsenic."

A. More.

R.R.

June 14, 1923.

Biological Observations on the Government Chemist's Report.

It is interesting to compare the biological observations which were made relating to a few points discussed in the preceding report by the Government Chemist. With regard to the sample B in the green test-board (II), the high proportion of basic constituents referred to is almost entirely due to calcium oxide (see Table 2 (a), p. 434). It is certain that this excess is due to the inclusion of the calcareous test of Umbonula (see p. 432) which was growing on the bottom of the board and was included in the scrapings from the lower part of area B.

The low percentage of copper and arsenic in this sample is reflected in the occurrence of borings of gribble in area B; these borings give therefore a biological confirmation to the chemical analyses, for they occur nowhere else on the surface of the areas scraped.

The area A was scraped over a rather greater extent than was intended, and it included a small space where the paint was retained as in area D. Hence the average toxic constituents in area A was slightly higher than would occur where the hydroid growth was well developed.

It is noteworthy that excepting area A—which obviously became more rapidly denuded of paint due to the effect of the fixing nail the areas B, C, and D form a graded series from bottom to top of the board in loss of arsenic and copper. This series is continued at the bottom of the board by a non-toxic area on which organisms were growing abundantly and where doubtless the arsenic and copper had been washed out to a very great extent. It has already been pointed out that this board was fixed vertically with the bottom a little below the level of low-water mark of spring tides; thus there had occurred a graded erosion of the paint from the region of low water to 3 feet above. As the bottom of the board would be almost constantly in water, it would seem that the erosion of the paint was due either to greater wave action at the bottom of the board or possibly, in this particular situation, to greater chemical interaction with the sea-water in proportion to the longer period of immersion at the different levels of the board. The other test-boards in

this experiment also gave indication of maximum erosion at the bottom of the board (see Table IX, p. 402).

It is of interest to note that the reddish-brown paints have cuprous copper as the main toxic ingredient, while the green paint contains a large quantity of arsenious oxide, with a very high proportion of cupric copper, and with also rather more zinc than the aforementioned paints. The probable state of combination of these toxic ingredients is discussed in the Government Chemist's report (see p. 433).

Discussion of the Results.

The experiments herein described show clearly that a poisonous paint will inhibit the growth of marine animals for a period depending upon the retention of the paint on the surface it is desired to protect, and the existence in the paint of substances which maintain a toxic surface on the paint (see Table XV). It has been demonstrated that a dark green arsenic paint (II) remained toxic for a longer period than two red copper (IV and I) and one light green (arsenic) paint (XI), and that the durability of the matrix (oils, etc.) of the paint is a fundamental character of efficient paints. It is also clear that beyond a certain concentration of poison in a paint the durability of the matrix is more important than the nature of the toxic ingredient.

There can be little doubt that the best anti-fouling paints function through ionisation—and therefore loss—of the toxic ingredients.

Chemical analyses revealed the following facts with regard to a certain reddish-brown anti-fouling paint :—

	% Composition (approx.). Arsenious oxide.	Cuprous oxide.	Zinc oxide.
Original paint (IV)	0·2	11·8	0·5
(*a*) Toxicity retained after 19 months' exposure in the sea.	0·01	6 to 8	0·8 to 1·0
(*b*) Toxicity lost (some months previously) after 42½ months' exposure	nil to 0·05	0·2 to 0·6	0·5 to 0·6

Therefore the paint will remain toxic so long as it contains the ingredients of the order shown above in (*a*). Another dark green paint showed on chemical analysis :—

	% Composition (approx.). Arsenious oxide.	Cupric oxide.	Zinc oxide.
Original paint (II)	5·0	14·8	0·8
(*c*) Toxicity retained after 19 months' exposure in the sea.	2·6	16·6	0·04
(*d*) Toxicity retained after 42½ months' exposure (C, fig. 13)	0·7	7·5	0·4
(*e*) Toxicity recently lost after 42½ months in the sea (A, fig. 13)	0·4	4·0	0·2

Thus in order to maintain toxicity a paint of this kind must retain a concentration of the poisonous ingredients not less than the values shown in (*d*) above. In a similar way the combination of toxic ingredients which is necessary to inhibit growth of marine animals can be determined for any paint. The rate and nature of ionisation of the toxic ingredients at about the critical point for loss of toxicity has not been determined, but the non-toxic states of the two paints just noted indicate that a relatively high degree of ionisation of toxic substances is probably necessary to prevent the growth of animals on a surface in the sea. It has been pointed out that the results noted above were obtained under conditions more favourable than occur on the bottom of a ship where erosion plays a much more important rôle. In reviewing the extensive work done recently on this subject in America, Visscher (**16**, 1928) states that " Under optimum conditions vessels foul within 30 days of the time of dry-docking and the application of poisonous anti-fouling paints, indicating the hypothetical value of anti-fouling paints."

The experiment and observations herein described, however, indicate that good anti-fouling paints applied on a slightly roughened surface under dry conditions should give results which are definitely not hypothetical. It has, however, been demonstrated that great differences occur in the erosive value (i.e. degree of resistance to erosion) of anti-fouling paints (see Table XV, p. 422), and that paints such as VI or XI, be they ever so toxic, are probably of little value on the bottom of a ship. Hence the fundamental importance of the matrix of such paints. In the American work (*loc. cit.*) it would seem that the importance of the matrix has not been sufficiently recognised. It has been suggested herein that bacteria may be intimately concerned in breaking down both the matrix and toxic agents of a paint in the sea, and that researches on this subject are needed (see also Hillen, **24**, who found bacteria in the " slime " on ships' bottoms). If bacteria prove to be important destructive agents, then the constituents of these paints should have a low energy potentiality value, as Matthews (**17**) showed in analogous work on bacteria in soils.

The nature of the surface to which paint will adhere best has been shown to be a slightly roughened surface (see Table XV, p. 422). A rough surface is, however, undesirable on the bottoms of ships owing to the increase of frictional effect, but it may be possible to devise a method of coating a roughened surface with paint so as to leave a finished smooth surface. Paints applied to a very smooth surface are eroded or flaked off very easily (see Table XV). On non-toxic surfaces little difference has been found in these and other experiments in the *gross* growth, whether the surface be smooth or rough (see *passim* herein the growth on black varnish, IX, and the white smooth inner surface of scallop shells

on the one hand, and the growth on untreated wood and the outer rough surface of scallop shells on the other). I am, therefore, unable to agree with Visscher's remarks on this subject (**16**, p. 236), and consider that an alternative explanation is probable for each instance therein cited. It is obvious that the flaking of an anti-fouling paint will leave an area where organisms can and do settle (see especially Experiment H) and form a *point d'appui* for still other organisms. This is no doubt what has occurred in the case cited by Visscher (*loc. cit.*, Fig. 33B), and may be considered a silent tribute actually to the efficiency of the anti-fouling paint used in this particular case. The experiments described in these pages do, however, indicate that some hydroids—but not Tubularia—appear to grow better on a rough surface, but the evidence is not critical.

The effect of the nature of the light reflected from anti-fouling paints and other material has not been critically tested in these experiments, but in Experiments A to E heavy growths of Tubularia occurred within 6 weeks on greyish-white, red and black surfaces in subdued light. The correlated absence of growth on dark green and red poisonous surfaces is adequately proved to be due to the poisonous nature of these surfaces from the results of all the experiments. There can be little doubt that Tubularia will stick to any kind or colour of non-toxic surface in a subdued light, but the intensity of the light with regard to general growth is doubtless an important factor. In Experiment C, a growth of Algæ occurred on each of the green, red, and black painted and greyish-white untreated surfaces after 7 months' exposure (see Table III, p. 386), and a growth of Balanus occurred on a green paint in Experiment G after 9 months' exposure (see p. 415, and Holzapfel **25** and Visscher **16**, p. 240). It is probable, however, that light colours in well-lighted situations prevent such larvæ as Pomatoceros, Hydroides, and allied Polychaetes, most Polyzoan larvæ, the cypris of Balanids and the tadpoles of Ascidians from settling on them readily, but the actinulæ of Tubularia and the planulæ of hydroids appear to stick to any surface with which they come in contact; while the spores of Algæ prefer and require some degree of light (see raft observation, p. 398); it is, moreover, probable that although the tadpoles of tunicates undoubtedly fix in the darker places on experimental material in the sea they probably meet sufficiently dark places to induce settlement in the microscopic shade afforded by such growths as hydroids at even moderate depths on light-coloured surfaces (see Table XIV, p. 416). It is therefore probable that—other things being equal, an equality difficult to obtain—a light-coloured anti-fouling paint may inhibit the growth of marine animals *to a greater degree* than a darker paint, but may be expected to acquire a relatively greater fouling from algæ.

The surface of the paints exposed in the sea was observed and recorded. It was found that the best anti-fouling paints became eventually soft or powdery. The poorest paints became rapidly soft and easily eroded away, while the best paint, the dark green No. II, "powdered" very slowly and rubbed off slightly on the finger. Nos. IV and I paints remained hard—and clean—for many months but eventually became soft and eroded slowly. No. I eroded rather more quickly than IV. It is probable that the virtue in paint No. II lay in its capacity for powdering slowly and that the property is related mainly to the nature of the matrix, but possibly also to the interaction of the matrix and the toxic constituents. Any paint which relies on rapid erosion—and some are apparently constructed on this principle—is manifestly of little use on a vessel because of the rapid erosion (see Table XV, p. 422) to extinction.

It would appear that a soft or even slimy surface on a good durable anti-fouling paint is a necessity from the nature of the paint and its mode of functioning, and that it is therefore incompatible to strive for a hard and at the same time efficient poisonous paint. Visscher (*loc. cit.*) discusses the point from a different angle. He states that "the beneficial effects of the paints now used very probably can be attributed far more to the nature of the surface (when in water) than to any peculiarly poisonous property that they may possess. It seems that undue emphasis has been placed upon the use of poisons in paints on steel ships, which is probably a hold over from their use on wooden vessels, and that the proper nature of the surface film is the desired goal."

There can, however, be little doubt that the chemical analyses given of sea-exposed paints (at the beginning of this section, p. 438) at a point just before losing the power of inhibiting growth, and just after or at the instant of losing this power, is a demonstration of the dependence of these paints on toxicity for inhibiting growth. Therefore Visscher's conclusion is erroneous. The nature of the surface film of a paint may, however, be readily acknowledged as a property of primary importance.

On the Fundamental Properties of an Ideal Anti-Fouling Paint.

The experiments described in the foregoing pages have shown clearly that in order to maintain a painted surface free from marine growths it must be painted with a substance which requires to have three fundamental properties, namely :—

(1) It must adhere strongly to a surface which may be damp.
(2) It must present such a surface that marine organisms cannot exist on it (whether the surface be poisonous or otherwise).
(3) It must have the power of resisting erosion for a long period while retaining its inimical surface.

The power of resisting erosion for a long period will depend to a great extent upon the nature of the matrix, but also on the value of the other ingredients for preserving the matrix while maintaining a (toxic) surface on which marine organisms cannot exist. It may be presumed that marine bacteria are significant organisms in the disintegration of the matrix (researches on the bacterial infection of anti-fouling paints at different epochs of exposure have, however, not been made) of a paint, and that therefore the best matrix would be one highly resistive to bacterial action, while at the same time resisting chemical interaction with sea-water.

It would therefore appear that *beyond a certain concentration* the toxicity of an anti-fouling paint is less important than the property of resisting erosion, that is the longevity of the matrix. A paint may be intensely poisonous, but it is of little value if the matrix is such that easy disintegration and/or erosion occurs in the sea. If, as is suggested, bacteria are primarily concerned in breaking down the matrix of a good paint in the sea, then it appears that a fundamental property of the matrix must be a low-energy potentiality value, as Matthews (**17**) found to be necessary in the case of substances capable of resisting bacteria in soils.

The review of the results of the experiments given in Table XV, p. 422, affords an opportunity to see how the fundamental properties of an ideal anti-fouling paint are distributed among the substances tested. But as the life of any paint in the sea must necessarily be short in terms of years –being dependent upon the longevity of the matrix, it would appear that—failing the discovery of a permanent matrix—the problem of maintaining the bottom of ships clean and free from growths, for periods reckoned in years, must be solved by some other method than the application of paint.

PART III. OBSERVATIONS ON THE GROWTHS ON THE BOTTOMS OF OCEAN-GOING AND LOCAL SHIPS.

The following observations on the growth of marine organisms on the bottom of ocean-going and local ships within relatively short periods after being painted are useful as a practical indication of the inefficiency or efficiency of the paints used. In most of these cases the kind of paint used on the bottom of the ship was not known, but all were red in colour. If allowance be made, however, for the anti-fouling value of even inefficient paints the observations on the rapid growth of oceanic marine organisms and the transport of foreign organisms are well worth recording. Information regarding the duration and itinerary of the voyages

and the last dates of repainting were obtained from the masters of the ships, to whom acknowledgment is gladly and warmly tendered.

S.V. *Jarstein.* Master, A. B. Axelsen. Examined at Plymouth September 2nd, 1913.

Painted with tar and a copper paint at Pelotas, South-east Brazil, May 16th, 1913, but only passed into salt water June 17th, 1913, on crossing the bar of Rio Grande (see the South American Pilot, Part I, p. 354, Admiralty).*

The following growths on the bottom of this ship were collected at Plymouth on September 2nd, 1913 ; the maximum age of this growth is therefore only eleven weeks :—

Species.	Length of peduncle.	Breadth of capitulum.	Sex condition.
Lepas Hilli	35–60 mm.	13–20 mm.	Mostly with ova or embryos.
Lepas anatifera	29–55 ,,	11–18 ,,	do.
Conchoderma virgatum	25–33 ,,	9–10 ,,	Mostly with ova or embryos and some with nauplii.

A specimen of *Nautilograpsus minutus* was taken on the stern of this ship, having a carapace width 11 mm. and length 10·5 mm., but may have either settled on the boat as a larva or at a later stage.

S.S. *War Viceroy.* 2nd Officer, G. Bryant. Examined at Plymouth, September 25th, 1919.

Docked and painted March, 1919, at Cardiff ; left Venice for Australia end of April, 1919 ; left Geelong for Plymouth, July, 1919, via Albany, Durban, Cape Town, St. Vincent, Cape de Verde Is., and arrived Plymouth, September, 1919. Average speed 8·2 knots, maximum $10\frac{1}{2}$ and minimum $5\frac{1}{2}$ knots.

The maximum age of the following is, therefore, about 5 months, i.e. May to September :—

			Peduncle.
Lepas Hilli, length and breadth of capitulum		27×16 mm.	ca. 22
Conchoderma virginatum	do.	22×15 ,,	ca. 25
,, *auritum*	do.	23×14 ,,	ca. 36

Balanus sp. probably *tintinabulum* with test 20×19 mm., subcircular at base and height 18 mm.

Tubularia sp. abundant.

* For this reference I am indebted to Commander Campbell Hepworth, the then Marine Superintendent of the Meteorological Office.

Lepas and C. *virginatum* had embryos in the brood pouch, but *C. auritum* had only ova, which are apparently attached to the lining of the mantle cavity.

s.v. *Miefield*, Liverpool. Capt. Drummond. Examined at Plymouth, April 7–14th, 1913.

After spending about 6 weeks in fresh water at Buenos Aires and directly afterwards about 2 months in fresh water at Newcastle, N.S. Wales, this vessel returned to Plymouth via Anto-Fagasta, Chili, and Falmouth with only short periods at each of the ports. The ship was last painted on the bottom at Fiume, Austria, in June, 1911.

The age of the material cannot be given, but it is certainly not more than 4 or 5 months ; growth doubtless began soon after leaving Australia on a bottom probably denuded of paint. The vessel was steel, not wood.

Conchoderma virgatum, some with embryos and nauplii with capitulum only 15×10 mm. and others much larger.

Conchoderma auritum, eggs in peduncle and apparently in the mantle lining (capitulum 25×16 mm., peduncle 50 mm.)

Lepas anatifera, some with nauplii (capitulum 35×21 mm., peduncle 20 mm.).

Lepas Hilli, some with nauplii (capitulum 30×18 mm.). Cellularia sp., Tubularia sp., and Amphipods in nests covered the bottom of the ship.

Nautilograpsus minutus, the Sargasso seaweed crab ; three specimens ; two escaped ; one male with carapace width 10·5×10 mm. long.

Pilumnoides perlatus, a South American crab ; twenty-one specimens ; some were soft and some were moulting in April ; the four largest specimens were males with carapace width 9 mm. ; seven others were males, seven others females, and three of undetermined sex. These specimens were exhibited at the Royal Society Soirées in 1913, and on August 26th, 1913, the remaining females had grown to carapace breadth 12 to 14 mm. ×9 to 11 mm. in length, and a male 9×7 mm.

Concholepas peruviana, a Chilean Gastropod, was taken (one specimen) creeping on the bottom of the vessel.

By adding powdered carmine to the water in which *C. auritum* was kept it was observed that water was drawn in at the auriculæ when the animal exserts its cirri, and expelled when the animal retracts into its shell. There can be no doubt therefore (as Darwin suggested, **26** II, p. 145) that one function of the auriculæ is connected with respiration. Observations are, however, required on the orientation of the auriculæ in relation to the direction of motion of the vessel and on the feeding mechanism, before the function of these peculiar organs can be understood.

s.v. *MacMahon*, Nantes. Capt. Guteguiz.

This vessel was painted on April 15th, 1913, and examined for growth at Plymouth, October 17th to 20th, 1913, so that the maximum age of growths on the bottom is about 6 months, but as the paint would have some anti-fouling value, the actual age must be much less than this period. Lepas and Conchoderma, hydroids and spawning Nudibranchs were collected from the bottom of this vessel.

s.s. *Penolver*. Capt. Bradshaw.

This vessel was painted with a well-known red anti-fouling paint and left Barry Dock at the end of January, 1920. It arrived at Rio de Janeiro, February 25th, and left March 3rd, 1920; arrived Buenos Aires 9.3.20 and left 10.4.20; arrived St. Vincent 29.4.20 and left same day, reaching Plymouth May 12th, 1920. A few pedunculate barnacles were collected from this ship at Plymouth, May 19th, 1920, only $3\frac{1}{2}$ months after being painted with an anti-fouling paint.

s.s. *Wotan*. Master, Fred Hancock.

This vessel was dry-docked and received two coats of anti-fouling paint at Glasgow, December, 1919, and proceeded to Barry, Malta, Constantinople, Sevastapol, Odessa, Salonica, Gibraltar, and thence to the River Plate, arriving there April 10th, 1920, and loaded up the River *in fresh water*. The ship sailed for Plymouth, May 1st, arriving June 7th, 1920.

A number of Lepas and Conchoderma, the latter of which were carrying embryos, as well as some South American crabs, were taken from the bottom of this vessel. These barnacles had undoubtedly grown since May 1st, that is in only 5 weeks and 2 days, and attained sexual maturity on a bottom painted so recently as $5\frac{1}{2}$ months.

s.s. *London City*.

This vessel was docked and painted at West Hartlepool, April, 1910, towed round the coast to Brixham, and used there as a coal hulk. The bottom of this vessel was examined at Plymouth on August 1st, 1911, and an exceedingly luxuriant growth found of Tubularia, Pomatoceros, and other worms, numerous *Echinus miliaris* up to a diameter of 3 cm.; abundant *Sagartia viduata* (=*anguicoma*) with a column uniformly ca. 20 mm. in diameter and 4·5 cm. high (preserved); numerous *Dendronotus frondosus* upwards to 40 mm. long (preserved) were found feeding on the *Tubularia larynx*.

The maximum age of growth on the bottom of this vessel was 16 months, but the actual age must have been very much less for most of

the growth, such as Echinus, Sagartia, and Dendronotus. For information regarding this vessel I am indebted to Mr. T. E. Gullett.

s.s. *Smeaton.* Master, J. J. B. Hambley.

This vessel cruised only locally and was observed over three docking and painting periods.

It was scraped and painted April 18th, 1912, and examined in dock on November 25th, 1912, only 7 months later. On the latter date a heavy growth was found of Balanus, mature Pomatoceros, larvigerous Bugula, Ciona up to 3·3 cm. (extended) which gave larvæ on artificial fertilisation, Molgula which gave some segmenting eggs, and Anomia which gave some larvæ on artificial fertilisation.

On November 27th, 1912, the vessel was refloated and redocked April 23rd, 1913. On this date only a few patches of hydroids occurred on the bottom along with a few small Mytilus.

The contrast in these two periods, one summer and one winter, is very marked. The actual paint used is not known, but believed to be red oxide.

s.s. *Sir Walter Raleigh.*

Docking and painting occurred November 12th, 1912, and a subsequent redocking for painting May 14th, 1913, that is after 25 weeks. Only a very slight growth was again found, as occurred in the winter period with s.s. *Smeaton.* Two patches only of Tubularia occurred, a few Balanus, one colony of Bugula, two or three specimens of Pomatoceros, but many patches of a hydroid, probably Gonothyræa, up to 9 inches in diameter. The paint used in this case was probably also red oxide.

No. 1 *buoy,* timber with zinc, G.W.R. Docks, Plymouth.

The date this buoy was put out is uncertain, but on the zinc and timber were numerous clear-tested Ascidiella up to 6·5 cm. long, living and expanded, Ciona up to 8·6 and numerous smaller ones (expanded), much Botryllus, and fine long colonies of a hydroid, probably *Obelia longissima.* Similar zinc buoys exposed for two or more years acquire luxuriant growths similar to those described on the Cawsand Bay raft (see p. 398).

No. 10 *buoy* (iron), G.W.R. Docks, Plymouth, newly painted with red oxide, May 14th, 1913, was examined May 8th, 1914, and found to have only small Ascidiella, a few Mytilus, but large colonies of Botryllus and Diplosoma and a heavy growth of seaweeds. Heavy growths have been found on many similar buoys after exposure of the paint from 1 to 2 years.

ACKNOWLEDGMENTS.

In the prosecution of the large amount of experimental field-work herein described, I am greatly indebted to Mr. Wm. Searle for valuable advice and willing assistance in many ways.

The chemical analyses undertaken by the Government Chemist and his staff in connexion with this work served the dual purpose of providing valuable additional data for these and other investigations. In so far as the chemical results obtained assist my own work, I owe and gladly tender thanks to those workers, and especially to Sir Robert Robertson.

For the photographs which illustrate the paper I have pleasure in thanking Mr. D. P. Wilson, who took most of his photos by flashlight, and Mr. A. J. Smith, and for other assistance in photography I gladly acknowledge help by Prof. J. S. Dunkerley and Dr. R. S. Clark. I am also indebted to Mr. F. S. Russell and Miss M. Lewis for assistance in reading the proofs.

SUMMARY.

Contemporaneously with extensive researches on the rate of growth and breeding in marine Invertebrates, observations were made on experimental material exposed in the sea for periods varying from 14 months to $3\frac{1}{2}$ years to test the power of a number of paints and other substances (1) for inhibiting the growth of marine organisms, (2) for their preservation value, and (3) for their durability in sea-water. The experimental material was tested simultaneously in seven different habitats in three different localities on wood and on shells, which provided three essentially different types of surface.

The substances tested include proprietary anti-fouling and proprietary anti-corrosive paints, other anti-corrosive and preservation paints, coal-tar, varnish, some common paints, sheet copper, and sheet zinc.

Observations were also made at Plymouth on the growth on the bottoms of ocean-going ships, and on local ships, buoys and rafts.

It was found that certain proprietary anti-fouling paints did not inhibit the growth of marine animals under the conditions of the experiments for more than a few weeks. Other similar paints inhibited the growth of marine animals for about 9 months, while others inhibited such growths for periods varying from 20 to $42\frac{1}{2}$ months.

The so-called anti-fouling paint which inhibited growth only for a few weeks was non-toxic; the paints which inhibited growth for longer periods were toxic, and their toxic property depends upon the maintenance in the paint of toxic ingredients of a certain concentration.

Some of the toxic paints eroded so rapidly that the prepared surfaces

became denuded of paint before the toxic properties were lost: in other paints erosion occurred sufficiently slowly in some situations for the toxic effect to be lost before the paint was completely eroded. Chemical analysis of two paints which had been in the sea for 19 months without permitting overgrowth on the paint, and of the same two paints at a later epoch when overgrowth had occurred, or was just beginning, gave the following results :—

		Poisonous constituents. Percentage composition.		
		Arsenious oxide.	Cuprous oxide.	Zinc oxide.
No. IV.	Paint exposed 19 months without overgrowth	0·01	6 to 8	0·8 to 1·0
No. IV.	Paint exposed 42½ months with overgrowth aged some months	nil to 0·05	0.2 to 0·6	0.5 to 0·6

		Percentage composition.		
		Arsenious oxide.	Cupric oxide.	Zinc oxide.
No. II.	Paint exposed 19 months without overgrowth	2·6	16·6	0·04
No. II.	Paint exposed 42½ months without overgrowth	0·7	7·5	0·4
do.	do. with overgrowth	0·4	4·0	0·2

These analyses fix for these particular paints the approximate limits of the toxic ingredients which are necessary to maintain toxicity, and also prove that these paints inhibit marine growths by maintaining a toxic influence at the surface of the paint.

In the case of the paints No. IV and No. II, which are shown to be good or excellent anti-fouling preparations, these paints, as well as other preparations, adhered well to the rougher surface of scallop shells and to glass-papered dry wood, but very badly to the smoother face of the scallop shells. Anti-fouling paints must therefore possess the following fundamental properties :—

1. Capacity to adhere to a surface, which in practice may be slightly damp.
2. Capacity to resist rapid erosion.
3. Capacity to prevent continuously—whether the vessel be stationary or in motion—the settlement and growth of the larvæ of marine organisms (a capacity usually attained by the incorporation of toxic ingredients).

Some of these fundamental properties may be modified to meet economic conditions, e.g. painting the bottoms of ships in dock in a hurry ; but some of the economic conditions must be modified to meet the inherent deficiences of anti-fouling paints, e.g. a sufficiently thick deposit of the

paint must be applied to a dry and rough surface to ensure adherence, to resist erosion, and to maintain a toxic surface for a reasonable period.

It is pointed out that in order to resist erosion the body of the paint must be durable, and that the durability of the body may be largely conditioned by the attacks of marine bacteria and the energy available in that body. The body used in the construction of these paints is highly important, and the experiments described prove that certain proprietary anti-fouling paints are fundamentally deficient in possessing a body incapable of resisting even a moderate amount of exposure to sea water.

Thus the body of a paint may be more important than the toxic ingredients subject to the maintenance of a certain degree of toxicity.

It is shown that marine organisms can live and flourish adjacent to paint residues which give on chemical analysis high percentages of (presumably) toxic substances, but that further investigations are required to give the rate and degree of ionisation of the toxic ingredients at the surface of a paint at various epochs after the date of first exposure in the sea. Anti-fouling paints exposed to strong light permit growths much sooner than in subdued light, but in the former case the growth is marine algæ. It is pointed out that it is not clear whether this phenomenon is due to loss of toxicity in the paint due to the direct action of light, or to a greater resistive power of the spores of marine algæ to toxic agents. It is suggested that all toxic substances before or after combination with organic matter may be attacked by bacteria in the sea, and that such substances may therefore undergo a regular "life-history" of degradation and that in this respect copper may be short-lived.

The preservative properties of the substances (paints, coal-tar, etc.) were investigated on test-boards in one critical situation where wood is rapidly eaten away by gribble (i.e. Limnoria and Chelura). It was found that the substances range themselves into three categories.

A. Definitely anti-fouling and definitely preservative (on wood).
B. Non-anti-fouling but definitely preservative (on wood).
C. Slightly anti-fouling and slightly preservative (on wood).

It is pointed out that the experiments are subject to certain limitations in comparison with economic practice, in that none were carried out on iron. The variety of surface tested, however, permits proximal deductions regarding the behaviour of the substances on iron.

Thus Classes A and B (above) are -when properly applied—probably also good anti-corrosive agents on iron, as well as being valuable preservatives on wood.

Class C, in which occurs Red Oxide (of iron)—the commonest and most widely used of anti-corrosive paints for the bottom of iron ships,—is definitely shown to be of less value than either A or B on wood, and is also

probably of less value than these on iron owing to weak resistance to erosion.

Class B includes common coal-tar, and common black varnish, while Class C includes, besides Red Oxide, certain proprietary anti-fouling and anti-corrosive paints and an ordinary aluminium paint.

Preservation is manifestly distinct from anti-fouling, though both may be effected by the same paint. The preservation of wood (by paints) can be ensured against "gribble," but not against Teredo, by common coal-tar and black varnish, to at least as great a degree as by the application of many special paints and "Red Oxide." On the other hand, well-dried coal-tar and black varnish give innocuous surfaces on which marine organisms establish themselves more readily in the sea than on untreated wood, the latter substance being usually slightly inimical to growths for a short period. It was found that all the paints and other substances adhered better to a rough than a smooth surface in all the experiments. Hence the conclusion that the bottoms of ships should be slightly roughened before the application of a paint, and the paint itself applied in such a way as to produce the smooth surface required for the reduction of friction. Coal-tar is proved to be a valuable preservative against gribble, but Teredo bored almost at once into wood which had been covered with two good coats of well-dried coal-tar. In these cases the larvæ of Teredo had either bored through the coal-tar, or not improbably had found spots in the wood imperfectly covered with tar.

The paints in preliminary experiments were found to adhere less well to a damp than a dry surface; it is therefore recommended that after scraping and brushing, *the bottoms of ships should be well hosed with fresh water* and allowed to dry thoroughly (ideally) before the application of a paint.

The composition of an ideal anti-fouling paint is discussed, but the conclusion is reached that if the bottoms of ships are to be maintained free from growths for a period, stated in years, some other method must necessarily be used than the application of paint.

Observations are recorded of the rapid fouling of the bottoms of local ships treated in the spring with red oxide and relatively little after an equivalent period when treated in the autumn with the same material.

Heavy growths are recorded on rafts treated with coal-tar, slighter growths on buoys painted with a red paint, and on zinc buoys, within a period of about a year. A growth of Conchoderma and other barnacles which attained sexual maturity in a minimum period of 5 weeks and 2 days is recorded along with other rapid growths on ocean-going ships inspected at Plymouth. The capture of the Sargasso seaweed crab, *Nautilograpsus minutus* (=Planes), of the South American crab, *Pilumnoides perlatus*, and the Chilean Gastropod, *Concholepas peruviana*, on the bottoms of ships arriving at Plymouth is also recorded.

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The Larva of *Nicothoë astaci* and its Systematic Position.

By

Robert Gurney, D.Sc.

With 6 Figures in the Text.

Mr. Leigh-Sharpe, in his account of the external structure of this interesting Copepod (1926), concludes that it is most nearly related to the Ascomyzontidæ. Having recently obtained a number of larvæ, hatched from adults obtained at Plymouth, and finding that my own conclusion as to the relationship of the genus differs from that of Mr. Leigh-Sharpe, it seems worth while to describe the larvæ and the bearing they seem to have upon the systematic position of the adult.

The larvæ hatch and become active inside the egg-sac.* Immediately after becoming free they swim vigorously for a short time, but very soon sink to the bottom and remain quiescent, with occasional spasms of activity. This quiescence may, of course, not be normal; but, as the larvæ remained alive for over a week, their behaviour during the first days cannot be due to ill-health. One may suggest that this is the normal procedure; the early activity ensures some dispersal and the later rest on the bottom brings them into touch with a new host. I have seen exactly the same thing in the larvæ of *Chondracanthus lophii*. As hatching proceeded the beaker in which they were contained became filled with swimming nauplii; but the next morning all were on the bottom and there remained, apparently perfectly healthy, and readily stirred to sudden spurts of movement, for several days.

The larva hatches as a Cyclopid with two pairs of legs and a rudimentary third pair. (Fig. 1.)

Length: ·28 mm.

The cephalothorax is as long as the rest of the body, and includes the somite of leg 1. The somites of legs 2 and 3 are free, and are followed by two legless somites. Furcal rami short, bearing 6 setæ, 1 dorsal and 5 lateral and terminal. The innermost seta is the longest, and between it and the next one is a delicate sensory seta. No eye is visible.

The antennules are of 3 joints (Fig. 3), the third the longest and bearing numerous setæ. The antennæ are difficult to make out, but appear to

* This has already been noted by Rathke, 1843.

consist of four joints, the last two flexed upon the second (see Fig. 3). The last joint ends in a spine and bears an inner seta. The mandibles are enclosed within the mouth tube, which has the form of a sucker. The distal part of the sucker consists of a chitinous ring strengthened by radial thickenings. The ring is enclosed by a transparent membrane broken at its outer edge into a very delicate fringe. In the bottom of the conical hollow can be seen the mouth opening through which the tips of the mandibles protrude. While the distal disc is entire, except

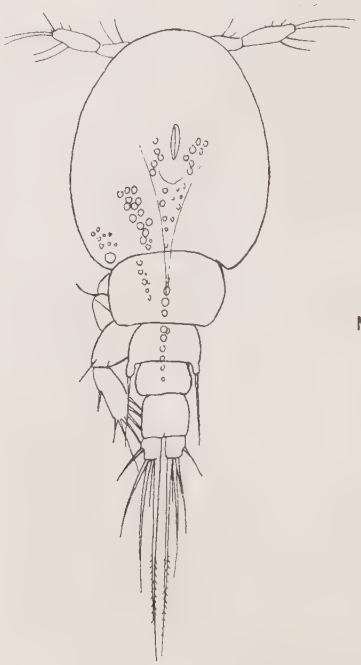

Fig. 1.—Copepodid larva, dorsal view.

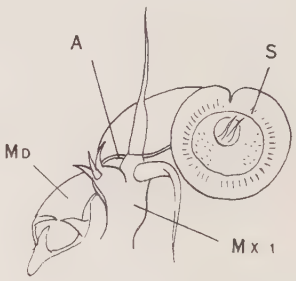

Fig. 2.—Side view of sucker. S. sucker. A. lateral suture of sucker. Md. mandible. Mx. 1. Maxillule.

for an anterior median indentation, the mouth tube itself is made up of an anterior and a posterior part, representing the upper and lower lips, the division between them being marked by a distinct suture visible in side view (Fig. 2). The mandibles, which are hinged to the body close to, and outside, the base of the maxillules, pass into the mouth tube through a gap in the suture.

Close against the antennæ and just behind the sucker is the maxillule. This is made up of two parts. Quite distinct is a small papilla bearing three short spines, and on the inside of this is a cylindrical joint bearing two long flagella.

The maxilla is a strong three-jointed appendage, situated some way behind the maxillule. The basal joint is very broad, and is followed by two simple narrow joints, the distal one with a brush of spines at the end.

The maxillipede is four-jointed, the last joint bearing a strong claw and a seta.

The two pairs of swimming legs are biramous, the branches one-jointed. The third pair is represented by a bilobed rudiment, the outer lobe being a small papilla, visible dorsally, bearing one long seta.

In the adult there is no essential difference in the arrangement and structure of the mouth parts (Fig. 4). The sucker seems to be rather more

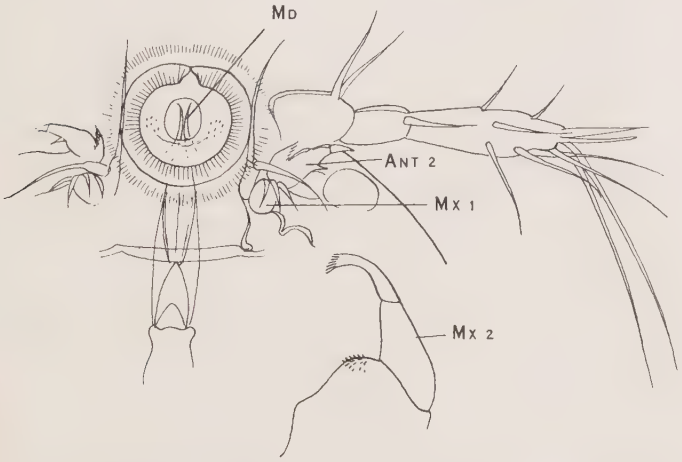

Fig. 3.—Copepodid. Ventral view of head region. Ant. 2. Antenna. Md. Mandible. Mx. 1. Maxillule. Mx. 2. Maxilla.

complicated, and on either side of the mouth, in the sucker-cone, is a pad covered with minute prickles.

The maxillule has much the same form, but there is now a third flagellum on the anterior branch of it (Fig. 6).

In Mr. Leigh-Sharpe's figure of the adult there are two structures shown which should be mentioned, namely, the second antenna and the pair of "lunules."

In a specimen cleaned with caustic potash both these structures can be seen and appear to be chitinous bodies enbedded in the carapace. The "lunules" show no resemblance to the lunules of Caligus to which he has compared them.

As regards the systematic position of Nicothoë, Mr. Leigh-Sharpe points out a number of Cyclopoid features and concludes that it is a

member of the Ascomyzontidæ.* At the same time he gives as examples of Caligoid features the presence of "lunules," the suctorial mouth, and "a first attempt at the inauguration of a genital segment." I think the "lunules" can be dismissed, and the sucker-like mouth tube has much less resemblance to the mouth tube of Caligus than to that of some other Copepods.

It seems to me that the affinity is not with the Caligidæ nor with the Ascomyzontidæ, but with the Choniostomatidæ.

If a comparison is made between the larva of Nicothoë and that of a

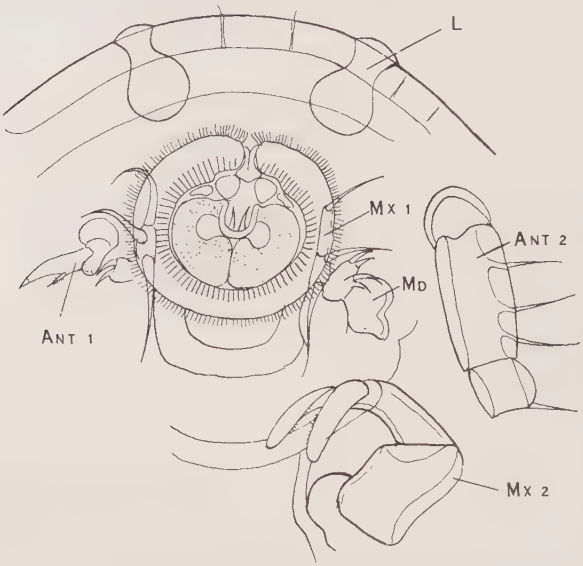

Fig. 4.—Adult female, ventral view of head region.
L. so-called Lunule.

Choniostomatid—e.g. Stenothocheres (Hansen 1897, pl. 1. fig. 1, 1) the agreement is almost startling. Apart from the general Cyclopoid form which in itself means little at this stage, we have a similar three-jointed antennule; the same form of mouth tube, with the same sucker; the same form of maxillule, and almost identical maxilla and maxillipede. In both cases there are two pairs of functional legs and a rudiment of leg 3, and the arrangement of setæ on the furcal rami is the same. The detailed structure of the maxillule in the Choniostomatidæ is not very clearly described or

* Leigh-Sharpe (1926, p. 153): "I consider it preferable to associate Nicothoë with the genera Pœcilopes and Lophiropes (with which, however, I am not yet acquainted) in the family Ascomyzontidæ (Asterocheridæ)." Compare Audouin and Milne Edwards (1826, p. 351): "Il n'est pas moins certain qu'il doit être rangé dans l'ordre des Branchiopodes de M. Latreille; mais il devient assez difficile de lui assigner une place plutôt dans la section des Pœcilopes que dans celle des Lophiropes."

figured by Hansen, but it seems to be built on the same plan and to include two or three flagella as in Nicothoë. The styliform mandible in both cases enters the base of the mouth tube and projects through the small mouth opening.

A further point of agreement is that in both larvæ there is a projecting median ventral ridge just in front of leg 1. This is very much more prominent in the Choniostomatidæ, and is named the "pouch" by Hansen.*

It may be no more than a coincidence that Nicothoë is parasitic in the gill chamber of a Decapod, and that all Choniostomatidæ are parasitic on

FIG. 5.—Antenna of adult female.

FIG. 6.—Maxillule of adult female.

various Crustacea, including some also in the gill chamber of Decapods; but it is a fact which should at least be thrown into the scale with the other resemblances.

In the Choniostomatidæ the copepodid larva becomes fixed to a host and moults directly into the degenerate form of the adult. We do not know the course of development in Nicothoë, but there is little degeneration in the adult, which has the full number of normal posterior appendages and the full number of abdominal somites. In the Choniostomatidæ not more than two pairs of legs are developed, and there is rarely in the adult any definite abdominal region. The antennules are of three joints,

* A similar, very prominent, ridge is found in the larval form known as "Saphirella," which probably belongs to the Clausidiidæ.

the second shortest and the third longest, exactly as in the larva of Nicothoë.

I suggest that Nicothoë represents more or less closely the primitive Choniostomatid form, and that the Choniostomatidæ themselves are really pædogenetic larval forms.

There is a striking tendency among the semi-parasitic and parasitic Crustacea to abbreviation of development, to which attention has already been directed by Canu (1892, p. 91). There may be only one or two nauplius stages, and the larva may seek a host in the first Copepodid stage (Lernæa) or the second (Ascidicolidæ).

Such early attachment to a host, before the development of the full complement of legs, seems to provide a condition most favourable to the occurrence of pædogenesis. There is, one might say, no inducement for the larva to develop legs or an abdomen which will never be of any use, and every advantage in the attainment of sexual maturity without further development. Garstang (1928) has interpreted the Appendicularians as pædogenetic Doliolids, and it is possible that this interpretation may be applied to other apparently " degenerate " animals.

The relationship of the Choniostomatidæ to other groups is a question still undecided. Hansen goes no further than to say that they come " much nearer to the Lernæopodidæ than to any other form of parasitic Copepoda " (p. 86). So far as the structure of the adult is concerned, there seems to be more affinity with the Ergasilidæ and Clausiidæ, but there is no doubt that there are points of resemblance between the larvæ of the Choniostomatidæ and those of the Lernæopodidæ and the Lernæidæ (and through the latter to the Caligidæ). Any real decision on this point involves a complete reconsideration of the parasitic and semi-parasitic Copepods. Such a revision must take into account above all the larval forms, and the possibility of pædogenesis must also be borne in mind.

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The Larval Stages of the Copepod Longipedia.

By

Robert Gurney, D.Sc.

With 10 Figures in the Text.

During a short stay at the Laboratory at Plymouth, with the object of studying the larvæ of Longipedia and Misophria, I was successful in identifying the nauplius of the former, and, as it is of rather exceptional interest from the systematic point of view, the various stages are described here. I did not find the adult of any species of Longipedia and am not able to describe the first nauplius with certainty, but the identity of the series as a whole was settled beyond doubt by the moulting of a late nauplius into a Copepodid which could be definitely identified as a species of Longipedia. It is impossible to say to which species it belonged, but the specific determination is not of serious importance.

All the stages described were taken in the plankton, in which they were common at this time (July 27th–August 7th, 1929). Three species referable to the same genus could be easily recognised by colour and to some extent by size and structure. The commonest form is of a dark green colour, with blue pigment dorsally, and it is from this form that the Copepodid moulted. It was generally to be found in plankton from the Sound, but was extremely common in a sample taken up the Tamar opposite the mouth of the Lynher. On the same day two other samples were taken lower down the Tamar, above and below the Docks, and the numbers of larvæ showed a very marked decline, indicating the upper waters as the home of the adult. Another form distinguished by its pink colour was very common in the Sound, but entirely absent from the Tamar. Isolated larvæ of this form unfortunately all died before the last moult, but in one sample in which the nauplii were unusually abundant a number of Copepodids were found which corresponded so exactly in their colour and the distribution of the pigment to the nauplius that there could be no doubt of their origin. A third form recognisable by its smaller size and yellow colour was also seen, but it was very rare as compared with the other two. It was found with the green form in the upper Tamar plankton. No Copepodid was found which could be referred to it. Only two species of Longipedia—*L. scotti* Sars and *L. minor* T. & A. Scott—have hitherto

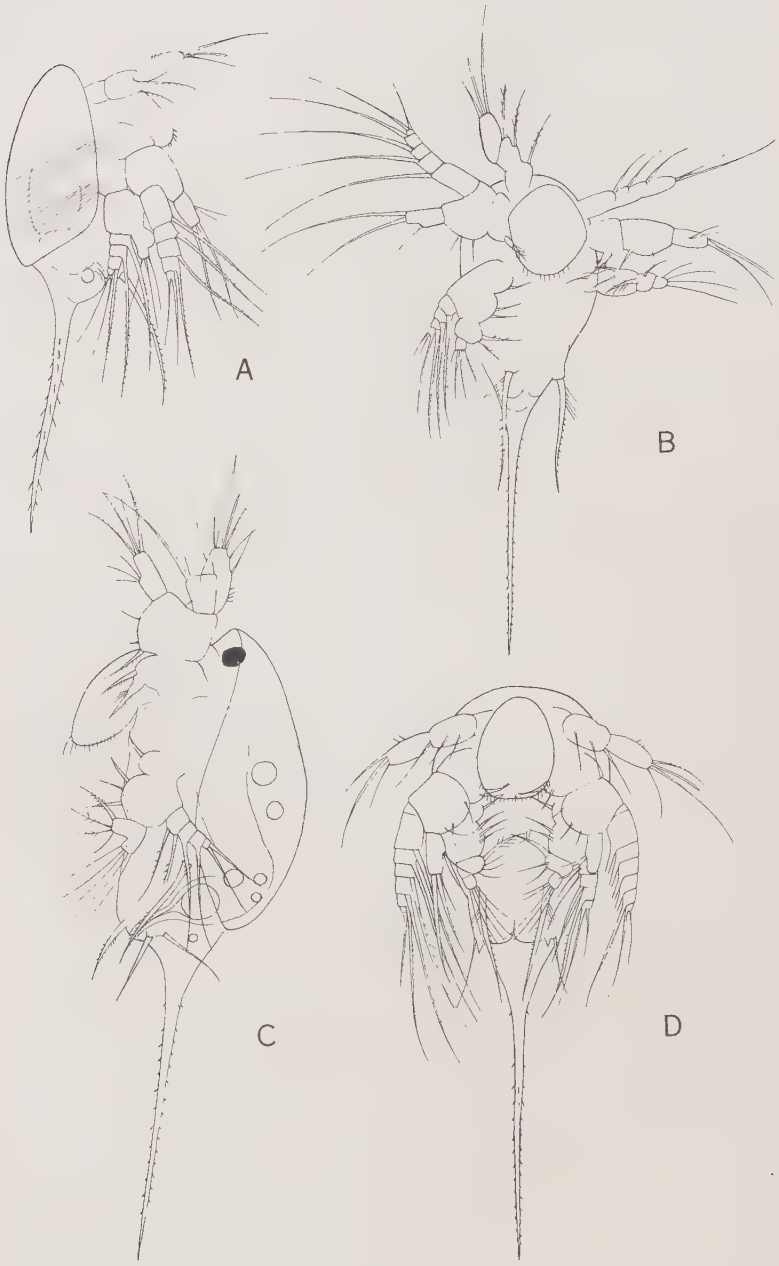

Fig. 1.—A. Longipedia, green form. Stage I, lateral.
B. Longipedia, green form. Stage I, ventral.
C. Longipedia, green form. Stage III, lateral.
D. Longipedia, green form. Stage II, ventral.

been recorded from Plymouth, but four are included by Sars in the fauna of Norway, and it is not unlikely that all of them may actually occur at Plymouth.

LONGIPEDIA SP. (Green form).

Stage I. (Figs. 1, A and B.)

Body pear-shaped, tapering behind into a spine which is longer than the body. In side-view the cephalothoracic shield is conspicuously marked. Labrum very prominent and fringed with short spinules.

Antennule three-jointed. Joint 1 bears one seta and joint 2 bears two, the three about equal in length. Joint 3 bears two setæ and an æsthete at the end but no lateral setæ.

Antenna with a long exopod of 5 joints, bearing 6 setæ, two on the last joint. The endopod is one-jointed, with a pair of lateral and two long terminal setæ.

The coxal joint has a single large swollen seta, and the basis has 4 small setæ.

Mandible with exopod of 4 joints, bearing 5 setæ, the proximal 3 setæ armed with spinules. Endopod of two joints.

Some distance behind the mandible, just in front of the anus, is a pair of very long curved spines, each with a brush of long hairs at its base. These may perhaps represent the future maxillules.

There are no furcal setæ, a very unusual feature.

Length : Body (to anus), ·125–·129 mm. Posterior spine, ·132–·144 mm. Total length, ·257–·273 mm.

Colour : At this stage the body is colourless or slightly greenish, with a conspicuous yellow intestine. Eye red.

Specimens of this stage, which I suppose to be the first, are very rare, and have only been found after much search.

In subsequent stages the general form remains the same, but the posterior spine becomes progressively shorter in proportion to the body, and the colour becomes conspicuously green, but with some blue pigment dorsally. The appendages remain much the same, but at each stage there are some differences in the number of setæ.

Stage II. (Fig. 1, D.)

Antennule—last joint with 3 setæ and æsthete.

Antenna—Exopod of 6 joints. Joints 1–5 with one seta, joint 6 with two. The first 4 setæ are feathered, but setæ 5 and 6 have a row of short spinules on the dorsal side only. Endopod with 3 terminal setæ. Coxa with a strong spine and a seta (fig. 3, A).

Mandible—Exopod of 4 joints, with 6 setæ, joint 1 having now 2 setæ. Setæ 2 and 3 are the strongest, and all except the first have short spinules.

Endopod of 2 joints, joint 1 with 4 setæ of which the basal one is strong with long feathering. Joint 2 with 5 setæ.

In the anal region there is a transverse ridge with a spinous process at each end, and a pair of short slender anal, or furcal, setæ.

The posterior spine has a circlet of spinules near the base which remains a constant feature of later stages.

Length : Body, ·175 mm. Spine, ·173 mm. Total, ·348 mm.

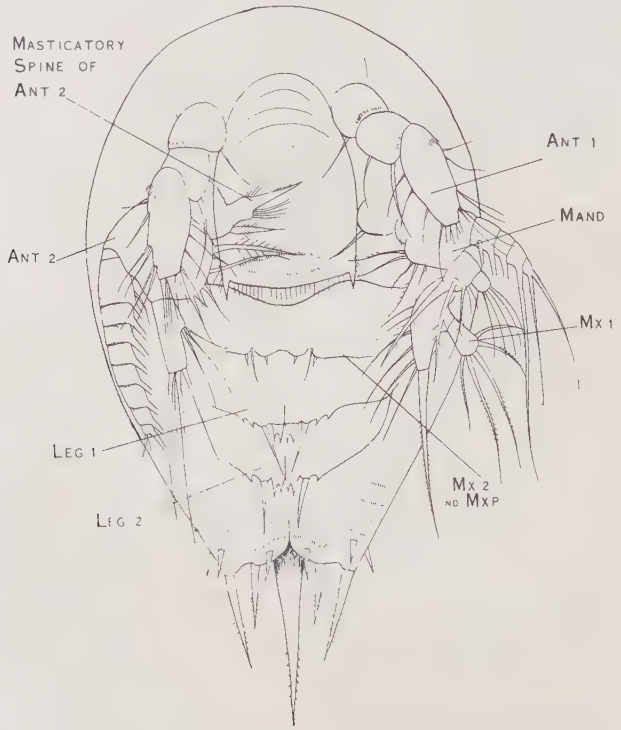

FIG. 2.—Longipedia, pink form. Stage VI, ventral. Antenna omitted on left side, and mandible and maxillule on right. Drawn from a moulted skin.

Stage III. (Fig. 1, C.)

Antennule—as before but with two short setæ on posterior, and one on anterior, edge of last joint.

Antenna—Exopod of 7 joints with 9 setæ. The first joint is divided at its base. This division is sometimes seen in Stage II. Coxa with two strong masticatory spines and a small seta. Basis with 4 setæ. Endopod with 4 terminal and 3 lateral setæ. Mandible almost unchanged.

The maxillule is traceable under the skin at the base of the long maxillular spines.

There are now two pairs of furcal spines in addition to the pair of furcal setæ.

Length : Body, ·188 mm. Spine, ·182 mm. Total, ·370 mm.

Stage IV.

Antennule—last joint with 3 anterior and 4 posterior setæ.

Antenna—Exopod of 8 joints. Endopod, etc., as before.

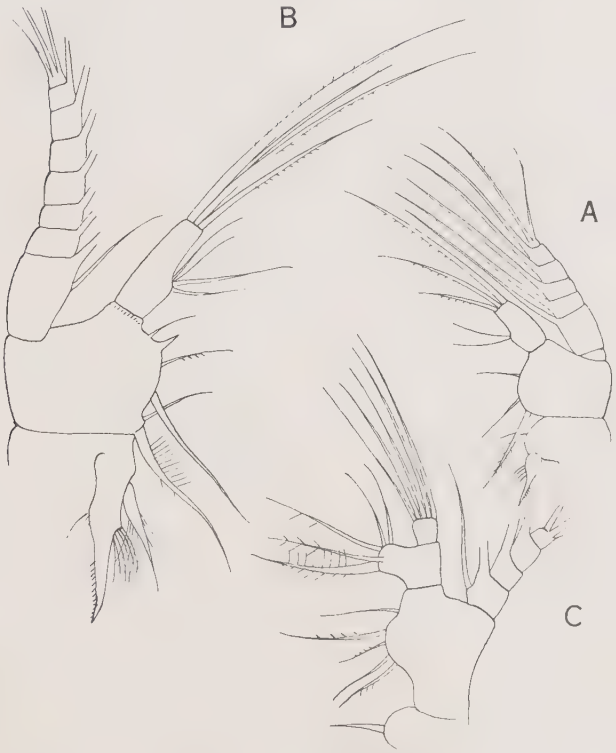

Fig. 3.—A. Antenna of Stage II, green form.
B, C. Antenna and mandible of pink form, Stage VI.

Mandible—Exopod of 4 joints, with 6 setæ. Endopod, joint 1 with 4 setæ, and joint 3 with 5.

Maxillule bilobed, the inner lobe with a strong terminal spine and 4 inner setæ ; the outer lobe with 3 setæ. Furcal region with 3 pairs of spines.

Length : Body, ·22 mm. Spine, ·19 mm. Total, ·41 mm.

This stage differs so little from the next that it is only separable with difficulty. At the same time I believe it does represent a distinct moult.

Stage V.

Antennule—last joint with 4 anterior and 6 posterior setæ.

Antenna—Exopod of 8 joints, with 11 setæ. Joint 1 has 2 and joint 8 has 3 setæ. Coxa with 3 setæ ; basis with 5.

Mandible—Exopod unchanged. Endopod, joint 1 large, produced inwards, with 3 strong and 2 slender setæ. Joint 2 with 5 setæ. Maxillule two-branched. Outer branch with 5 setæ ; inner with long stout terminal spine and about 6 slender inner setæ. Maxilla, maxillipede and two pairs of legs visible under skin. Three pairs of furcal spines present.

Length : Body, ·26 mm. Spine, ·18 mm. Total, ·44 mm.

Fig. 4.—Longipedia, green form. Cyclopid I, lateral.

Fig. 5.—Longipedia, green form. Cyclopid I, legs 1–3.

Stage VI. (Figs. 2 and 3, B, C.)

This stage differs only from Stage V in size, in the shorter spine, and in the appearance of the rudiments of the legs. The maxilla and maxillipedes are scarcely defined, their position being simply indicated by a transverse ridge with small spines and a pair of setæ. The two pairs of legs are represented by two ridges with spines, but are not definitely bilobed.

Length : Body, ·29 mm. Spine, ·185 mm. Total, ·475 mm.

The yellow form of nauplius does not appear to differ from the green one in any way except in colour and in being a trifle smaller. The pink form, on the other hand, is not only easily recognisable by its colour, but is also larger, and has a relatively shorter spine. It also differs from the other two species in having the labrum squarely truncated, with a spine at each angle, and in having a tooth on the basis of the antenna in addition to the usual setæ. (See Figs. 2 and 3 B.)

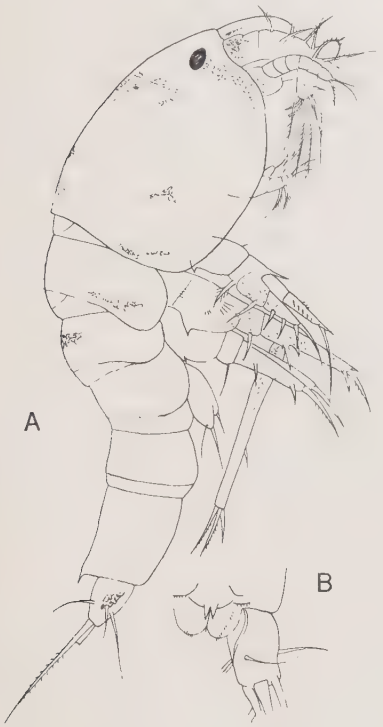

Fig. 6.—Longipedia, pink form. A. Cyclopid II, lateral. B. The operculum and furcal ramus.

Fig. 7.—Longipedia, pink form. Leg 2.

Cyclopid I. (Green form.) (Figs. 4, 5.)

Cephalothorax longer than rest of body. Rostrum very large and broad. Three free thoracic and one abdominal somite. Furcal rami rather long and narrow, with a pair of outer lateral spines, one long subterminal spine and two long terminal setæ. There is also a dorsal seta and a ventral spine. Anal operculum smooth.

Antennule of 3 or 4 joints, the basal joint indistinctly divided. As in

the adult, the antennule bears stiff bristly setæ, but they are relatively few. The last joint bears, in addition to several setæ, a pair of curved æsthetes as in the adult.

Antenna with large exopod of 6 joints, the endopod of 3 joints as in the adult. Mouth parts of the adult form.

Legs 1 and 2 biramous, the branches one-jointed. Leg 2 shows no sign of elongation of the endopod. Leg 3 is a bilobed rudiment.

Length : ·45 mm.

Colour : Thorax blue or blue-green, remainder colourless.

Cyclopid II. (Pink form.) (Figs. 6, 7.)

This stage differs from the preceding in having three pairs of legs well developed and a rudiment of the fourth. The fifth somite is distinct, but the abdomen is still of one somite. Leg 2 has developed the very long endopod characteristic of the adult. The operculum has a pair of median spines.

I have not seen this stage in the green form, but, among a number of cyclopids of the pink form taken in the tow-net on August 6th, one was found which had moulted to Stage II.

Other Allied Nauplii.

Besides the three forms mentioned above, which no doubt all belong to the genus Longipedia, two other types of nauplii have been seen which are evidently closely related, but must represent other genera.

Longipediidæ—Genus II. (Fig. 8.)

Only two specimens of this larva have been seen, both taken in the sample from the mouth of the Lynher, one in Stage I and the other in Stage V.

The resemblance to the larva of Longipedia in the structure of the appendages is so close that a near relationship is obvious, and there is also in Stage I the pair of large maxillular spines which is so characteristic.

On the other hand the body lacks altogether the conspicuous posterior median spine, and there is a pair of long furcal setæ in Stage I. The body has, otherwise, the same form as in Longipedia, with a very arched dorsal contour.

In Stage V the resemblance to Longipedia is still more marked. There are now 3 pairs of furcal spines, but no median spine. The larva is in fact simply a Longipedia without a posterior spine.

Length : Stage I, ·13 mm. ; Stage V, ·21 mm.

Longipediidæ—Genus III. (Fig. 9.)

Structure of appendages as in the preceding forms, and agreeing with Longipedia in having a long posterior median spine ; but differing from all other forms in the long narrow shape of the body and the remarkable helmet-shaped head. Not only is the head produced forwards and upwards, but it has also a downward beak-like projection. The labrum is very prominent and covered with small spines. Colour, rosy red.

This larva was fairly common in some of the plankton samples from the Sound, but I was unable to find any post-larval stage corresponding to it, or to keep the larva alive until the last moult. I found it almost impossible to isolate specimens alive, since they were almost invariably caught on the

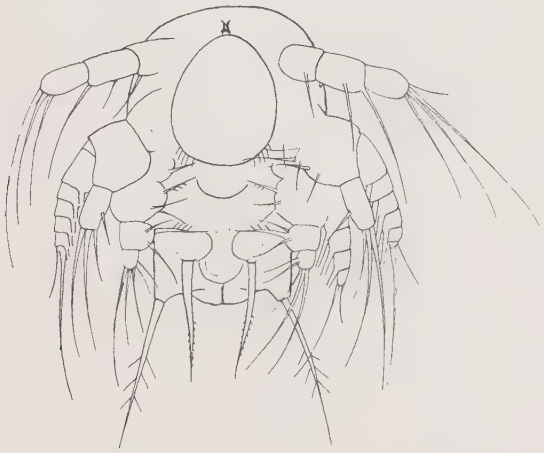

Fig. 8.—Longipediidæ, Genus II. Nauplius, Stage I.

surface film. The pink form of Longipedia has also a tendency to be so caught, but by no means so readily as this helmeted form.

While the identity of the Longipedia larva is beyond question, and the general relationship of all can hardly be doubted, it is impossible to assign the last two larvæ to genera. Prof. Sars includes in the family Longipediidæ the genera Longipedia, Canuella, and Sunaristes, and representatives of all these genera have been taken on the Devonshire coast. It may be no more than a coincidence that I find three generic types of larva ; but it is at least probable that " Genera II and III " represent the larvæ of Canuella and Sunaristes.

Discussion.

Prof. Sars, in his *Crustacea of Norway*, divided the Harpacticoida into two sections, the Achirota and Chirognatha, which are separated only

according to the structure of the maxillipedes. Within the former are included four families, Misophriidæ, Longipediidæ, Cerviniidæ, and Ectinosomidæ. The validity of this system is doubtful. In the first place a non-prehensile maxillipede is not confined to the Achirota, being found

Fig. 9.—Longipediidæ, Genus III.
Nauplius, Stage III.

also among Chirognatha in *Stenhelia palustris* (but not in other Stenhelias), Ceylonia, Viguierella, and Tachidiopsis. Secondly, it is difficult, apart from this character, to find within the Achirota anything by which to distinguish them as a whole from the rest of the Harpacticoida, and indeed it is very doubtful if these four families form a natural group at all. The Misophriidæ differ so much from all the Harpacticoida that they

should be regarded as forming a separate suborder, for they cannot be satisfactorily included either in the Calanoida or the Cyclopoida, though possessing some of the characters of both.*

Again, the relationship of the Longipediidæ to the Cerviniidæ and Ectinosomidæ does not seem to be very close. The Cerviniidæ include, in Sars' classification, the genus Zosime which resembles so closely some forms of the family Tachidiidæ (e.g. Tachidiopsis) that it is impossible to justify its placing in an entirely distinct section. Prof. Sars did not describe or figure the maxilliped of *Z. incrassata*, but it is in all other

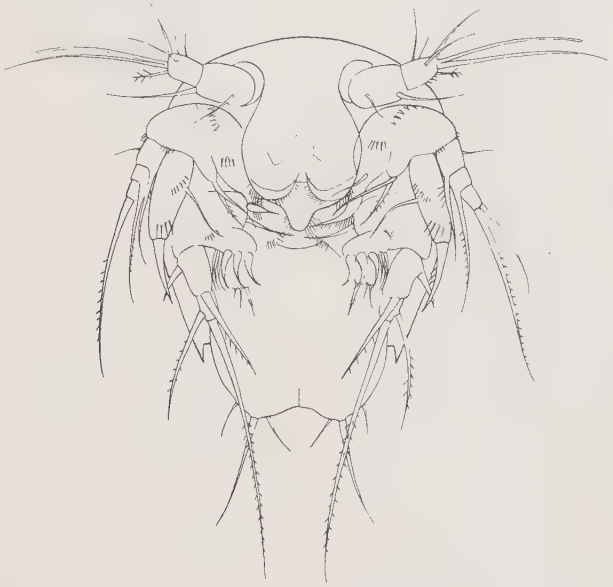

Fig. 10.—Nauplius of *Canthocamptus pygmæus* as an example of a typical Harpacticid.

respects a typical "Chirognath." The Ectinosomidæ are a well-marked family differing greatly both from the Longipediidæ and from typical Chirognatha.

So far as adult structure is concerned it seems that the division of the Harpacticoida into Achirota and Chirognatha cannot be sustained, and that the families included in the former are not very nearly related. Among them the family Longipediidæ is furthest removed from the Chirognath type.

In order to arrive at any sound grouping of the Copepoda it is certainly necessary that the characters of the nauplii should be taken into account,

* See Gurney, *Trans. Zool. Soc.*, XXII, p. 454, 1927.

and it is to be expected that a knowledge of the larvæ of the Achirota will throw some light on their relationship. Unfortunately we know at present only the larva of Ectinosoma, and that, while differing considerably from that of a typical Chirognath, is not so different as to justify a fundamental separation.

Having now made known the nauplius of Longipedia and two related genera, it is necessary to determine what evidence, if any, it offers with regard to the relationship of the family.

If we compare the nauplius of Longipedia with that of a typical Chirognath (e.g. Canthocamptus, Fig. 10) we find certain striking differences.

(1) The pear-shaped form of the body resembles that of a Calanoid and not the flattened discoidal form of a Harpacticid.

(2) The posterior median spine is seen in no other Copepod, but recalls that of the Cirripedes.

(3) The flattened form of the antennule is unique among Harpacticids, but exactly paralleled among Calanoida and, to a less extent, among Cyclopoida.

(4) The antenna differs from the typical Harpacticid type in the very long many-jointed exopod. In typical Harpacticids the exopod is relatively short and with not more than 4 joints. Even among the Calanoida and Cyclopoida it is rare to meet with an exopod so well developed, and it is only among the Branchiopoda, Cirripedia, and Penæidea that a parallel can be found. The endopod in most, if not all, Chirognath Harpacticids has become modified into a strong clasping organ, often very much larger than the exopod, while in Longipedia it is a simple one-jointed branch exactly the same, even to the arrangement of the setæ, as in Calanoida and Cyclopoida.

Lastly, there is a difference with regard to the coxa which it is a little difficult at present to take into account. In many, perhaps in all, typical Harpacticids this joint has a very large mandibular process which may be toothed at the end and appears to be a process of the joint rather than a modified spine. In Longipedia, as also is the case in Calanoida and Cyclopoida, this joint bears one, or in later stages two, stout movable spines of very different appearance.

(5) The mandible in typical Harpacticids always has the exopod more or less reduced. It is never so well developed as in Longipedia. The endopod is always more or less modified into a prehensile organ, the first joint bearing from one to three stout hooked spines and the second joint reduced to a small papilla bearing three to five setæ, or even absent, the setæ springing from the outer edge of the apparently single joint. In Longipedia the two joints are clearly distinct and there are no prehensile spines.

In this respect it seems to be more primitive even than the Calanoida where the two joints are usually fused, and to resemble more closely the Cyclopoida where they are distinct. It is in the Cirripedia that these joints are best developed.

In the Harpacticoida the basal joints do not seem to take any large part in mastication, having no mandibular process and only relatively weak spines. In this respect alone the limb of Longipedia resembles that of typical Harpacticids and differs from that of most Calanoida in which a mandibular process is developed very early. At the same time probably no great importance can be attached to this point, since the early development of the mandibular process in Calanoida (and also in Branchiopoda) seems to be a case of the early acquisition of an adult character and not primitive.

(6) With regard to the posterior limbs little can be said, especially as they belong rather to the adult than to the nauplius stage, but there seems to be a difference between the nauplii of Calanoida and all other Copepoda in that in them the maxilla and maxillipede may be quite distinct in the last nauplius whereas in other forms they are scarcely traceable. The appearance of a pair of spines representing the maxillulæ in the first nauplius in Longipedia is, so far as I know, a unique feature.

(7) The strong furcal spines developed in Longipedia are a feature distinguishing the nauplius from that of any Harpacticid yet described. It is only among the Calanoida that such spines are found, but in them there is usually some asymmetry of the furcal setæ which is not seen here.

This comparison makes it clear that, so far as the larvæ are concerned, the difference between Longipedia and such typical Harpacticids as we know the larva of is profound and much greater than it is between Longipedia and the Calanoida or Cyclopoida. In fact, anyone meeting with this nauplius and not knowing its parentage would almost certainly regard it as the larva of a Calanoid. It is true that the most conspicuous differences such as the very large exopodites of the antenna and mandible are such as may be accounted for by adaptation to a pelagic life, the nauplii of typical Harpacticids being creepers on the bottom ; but it seems more reasonable to regard these features as primitive. In Euterpina, a Harpacticid which is pelagic at all stages, the nauplius is a modification of the ordinary Harpacticid type, the exopods being enlarged without increase in the number of the joints. In this case there has probably been a secondary assumption of pelagic life. In the case of the Longipediidæ we have a family which has retained the primitive pelagic larva and has perhaps only comparatively recently become benthic as adults. It is worth noting that I have found species of Longipedia not uncommon

in plankton from the Suez Canal and from Samoa, and that it is an exceedingly active swimmer.

The general conclusion seems to be justified that, if there is to be any fundamental division among the Harpacticoida, it must be between the Longipediidæ and the rest. At the same time it is evidently premature to insist on such a conclusion until the larvæ of other forms such as Cervinia are made known and the identity of those here described as probably belonging to Canuella and Sunaristes is established. For the present it seems clear that the divisions Achirota and Chirognatha in Sars' sense should be dropped.

Incubation-habit in a Phyllodocid Polychæte, *Notophyllum foliosum* Sars.

By

Yô K. Okada.

With 1 Figure in the Text.

That a mother worm protects its eggs until the young are hatched is common enough among Polychætes, but not in the family Phyllodocidæ.

McIntosh (1908) mentioned in his *British Annelids*, Vol. II, Pt. I, p. 49, that two female specimens of *Notophyllum foliosum*, procured by his late friend Dr. Howden, at Lamlash, Arran, in August, were laden with mature eggs. Certainly the words " were laden " used here tell us something about the particular habit of the worm, but the sentence is too short and is not emphatic enough to attract attention. Hence his observation has remained without being noticed at all.

Using the opportunity of my stay at Plymouth, I have always paid attention to *Notophyllum* found among dredgings, and have carefully examined the specimens obtained, with the hope of proving McIntosh's statement. I was lucky enough to obtain two female specimens laden with eggs, and I am very glad to be able to prove the incubation habit in this Phyllodocid Polychæte. The accompanying figure shows one of these specimens mounted in Canada balsam.

This specimen was found in September, 1927, in an abandoned tube of *Serpula*, and measured about 12 mm. It consisted of fifty-six setigerous segments succeeded as usual by a pygidium. The dorsal cirri are exceedingly broad, which is a generic character, and they cover almost the entire dorsal surface of the body, overlapping one another on both sides. The lamellæ in the fresh condition are somewhat fleshy, soft, and rather yellowish in colour, with dark brown pigment round the edge.

When these broad dorsal lamellæ were turned forwards (or anteriorly), a mass of cream-like, yellow gelatinous substance came to light near the posterior end of the worm. A piece of this mass was isolated, and then brought under the microscope, which disclosed a large number of developing eggs, agglutinated together in a band or ribbon. The length of the entire band or ribbon extended from the 38th to the 47th setigerous segment or a little beyond these segments, and the band was fixed at both ends to the dorsal surface of segments 41–45 and

coiled in between these fixed points (see fig. 1). There was another small mass of the eggs attached near the level of the 15th setigerous segment, but in the second specimen such an anterior mass was not found. In other respects the incubation habit was the same in both cases.

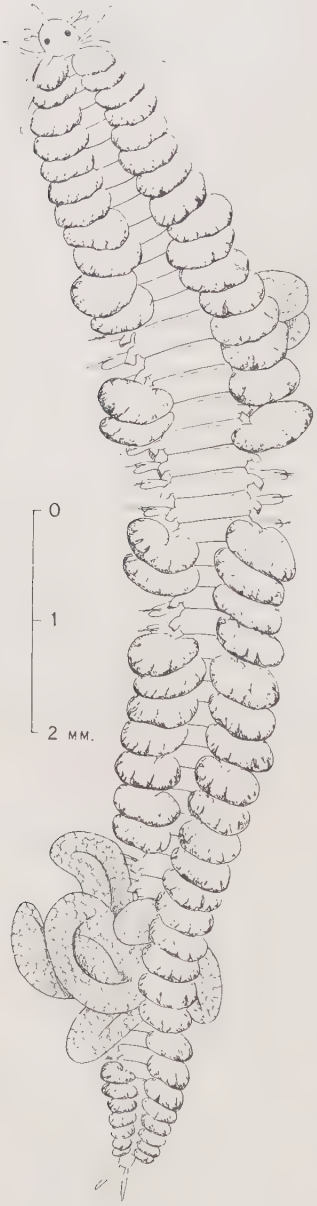

Fig. 1.

Without further description, it is easily understood that the method of incubation is the same or at least closely related to that of Polynoids. *Harmothoë imbricata*, a common Polychæte on both the English and French sides of the Channel, lives also in Japan, and there the worm incubates, protecting the eggs under the broad dorsal cirri or elytra, as they are called. According to A. Izuka (1912, p. 48), the breeding season of the Polychæte (at Misaki ?) is in "the months of March and April"; "the eggs are agglutinated together by a transparent mucous secretion," but not in the shape of a ribbon, and are carried under the elytra, from the 8th to the penultimate segment. The only difference to be found in this case is that the egg-masses do not form ribbons, and a greater number of segments is concerned in the phenomenon.

P. Fauvel (1916, p. 426) gives another example of a Polynoid showing the incubation habit in *Polynoë antarctica* from the Falklands. ("Sous les élytres, sont accumulés des œufs qui y paraissent incubés.")

The method of incubation in the Polynoids is evidently a special utilization of the space produced between the broadened dorsal cirri and the dorsal surface of the worm, but we are entirely ignorant as to why only a very limited number of species utilize this space for the special purpose of incubation.

In the Falklands collection Fauvel (l.c., p. 448) finds a specimen of *Cirratulus cirratus* in a tube

of *Potamilla* buried in the tissues of a sponge, protecting larvæ 2 mm. long. ("Ses branchies et ses filets tentaculaires, rabattus sur le dos et fortement emmelés, y retiennent une masse assez considérable de jeunes larves de 2 mm. de longueur, ne possédant encore que douze sétigères.") According to Ch. Gravier (1923, p. 179), this Polychæte does not incubate its eggs on the French side of the Channel, and I think perhaps not on the English side either. The incubation habit in this case of *Cirratulus* may be due to the low temperature at the Falklands, but the same analogy cannot be extended to the case of Polynoids, since at Misaki, Japan, where *Harmothoë imbricata* incubates, the water is by no means colder than in the English Channel.

If, on the other hand, the habit in question is a chance happening in certain Polynoids to utilize the comparatively wide space between the dorsal lamellæ and the surface of the body for the purpose of protecting the young, it would be little astonishing to find the same or at least a similar habit independently developed in Polychætes of another family having a similar differentiation of the dorsal cirri, and also utilizing the same space for the same purpose. The incubation-habit in Notophyllum would be of this nature, its origin, independent of, but closely related to the same habit of Polynoids. As mentioned by Gravier (l.c.), this method of incubation is the most primitive type among Polychætes.

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A Remark on the Constitution of Larval Syllids.

By

Yô K. Okada.

With 5 Figures in the Text.

The facts of Polychæte embryology inform us that the change of the trochophore into the perfect worm consists, first of all, in a growing out of the posterior section of its body and a gradual reduction of the anterior part, segmentation appearing at the same time. This phenomenon depends upon a marked change of the mesodermal bands, situated on each side of the intestine. Each of them is separated into two cell-layers, which spread out toward the mid-ventral and mid-dorsal lines. Then a segmentation makes its appearance in them, proceeding from in front backwards, and almost simultaneously the two layers of the bands separate from each other, by the formation of a cavity in each section or segment. That new segments are gradually formed one after the other, and from before backwards, in the hinder part of the growing body, holds true universally, but, at the extreme end a segment has been individualised from the first, or at a very early phase of the segmentation, and this segment does not divide again even to the end of development. In this way the pygidium is formed, and it represents the posterior individual portion of the trochophore. The growth of Polychæte-larvæ is therefore anteanal and entirely in the penultimate segment.

Syllids pass the earliest phases of their development within the egg-capsule, and the larvæ hatch out generally as metatrochophores, or even at the commencement of parapodial formation in the anterior secondary divisions or segments (*nectochætæ*). The origin of these new segments follows, of course, the law of embryonic development mentioned in the last paragraph ; this is, however, after the 9-meric stage in this family of Polychætes.

The larva of this stage has generally the following morphology : the prostomium has three appendages and two pairs of eyes on the dorsal aspect, but very frequently no palpi on the ventral side. In the second segment the dorsal cirri are well marked, but the ventral are either in an early stage of development or are not yet formed. The five following metameres are each provided with a pair of parapodia or those of the hinder part are replaced by bundles of setæ. Generally there are dorsal

cirri too. The larvæ of Exogoninæ are without the dorsal cirri in the second setigerous segment, and this fact seems quite constant within this sub-family (see Viguier's pl. V, fig. 52, 1884, or Malaquin's pl. XIV, fig. 32, 1893, for example). The eighth section of the body is the growth zone, and the ninth is the pygidium, which carries the already elongated caudal cirri.

Before this stage the larva, when typical, consists of seven segments, three being setigerous. Most larvæ of the Exogoninæ have this constitution (see Viguier's pl. IV, fig. 33, and Malaquin's pl. XIV, fig. 3).

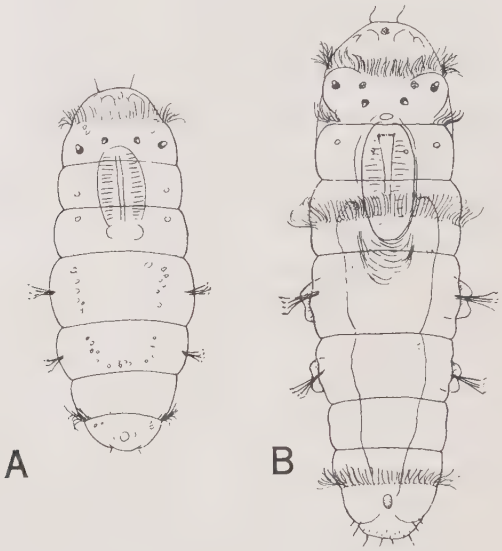

FIG. 1.—Larvæ of *A. longeferiens*, (A) one-day old and (B) four-day old, from Mrs. Sexton's sketches.

The growth zone being always penultimate, it forms here the sixth section of the body. However, a metameric number less than seven is usually normal, especially in the other sub-families, some being bi-setigerous (see Malaquin's pl. XIII, fig. 20 ; Herpin's pl. IV, fig. 92, 1925) and others mono-setigerous (see Malaquin's pl. XIV, fig. 17A ; Herpin's pl. VI, fig. 124 ; Greeff's pl. XIV, fig. 36, 1879). In such cases it is generally stated that the position of the setæ represents the third and fourth segments in the first instance, or the third segment alone in the second. My own view in respect to the position of the setæ in the atypical 7-meric larvæ of Syllids is different.

Dating back to 1914 (Feb. 18th) a Sacconereis of *Autolytus longeferiens* was captured by the tow-net off the Eddystone, S.W. by W., one mile (the Plymouth district). It carried two ovigerous sacs on its mid-ventral

surface, from which swimming larvæ were hatched out on March 2nd. Mrs. E. W. Sexton sketched several of them very faithfully from the living specimens. According to these drawings the larva of one day old, which is shown in Fig. 1A, judging from its matameric number, exactly corresponds to the 7-meric stage of the standard development. The larva in question is, however, bi-setigerous, pale yellow in colour and about 0·25 mm. in length. The cephalic section has two pairs of reddish-brown eyes and bears a ring of long cilia (akrotroch) in front of them. The telotroch (paratroch) appears on each side between the last two segments. The fourth section of the body is larger than any other, and this and the next segment are provided with setæ. The stomodeal invagination reaches the middle of the third segment and the intestine also commences from this position. It is almost impossible to doubt, unless we are deceived as to the exactitude of the sketch, that the anterior pair of the setose-bundles is formed in the fourth section, which corresponds to the second setigerous segment of later development, and the same is the case in the adult.

After three days the larva (Fig. 1B) (sketched March 4th) measures naturally more (0·35 mm.) than before, and several important changes have crept into its structure. A band of cilia appears in the middle of the third segment and surrounds it like a girdle (interparatroch). The telotroch is now complete all the way round, its position being between the last two segments as before. Another new feature is a band of cilia on each of the hinder borders of the cephalic section, just behind the position of the eyes (according to my reinvestigation this band is continuous on both sides, on the ventral side certainly, and it is almost without doubt the prototroch), and a new segment appears between the posterior setigerous segment and the penultimate growth zone. The pharynx and the intestine are as before. The setæ of the fourth and fifth segments are now elongate, and a primitive parapodium is beginning to be associated with each bundle of them. But neither of these organs is found in the third segment. This fact finally led us to investigate whether the segment bearing the interparatroch is really the third section of the larva, that gives rise later to the first setigerous segment of the adult worm. There is no sketch of the more advanced stages and no data are available to solve the problem.

Mr. D. P. Wilson has observed similar larvæ of *Autolytus pictus* in earlier phases than those of Mrs. Sexton, and by means of Mr. Wilson's observation we can trace two stages back. At the time of hatching (April 19th, 1927) the larva (Fig. 2A) was 0·25 mm. long and pale green in colour. There were neither appendages nor setæ in the body-segments. The eyes, four in two pairs, were only distinct in the head section, each provided with a prominent lens. The anterior lenses are directed forwards

and outwards, while the posterior look outwards and backwards. As a whole the larva is elongate and pyriform, the wider end being anterior, and it is divided into five sections. The prototroch is well marked and is situated behind the eyes. It is transversely straight on the dorsal surface, while, ventrally, it is continuous and arches forwards in front of the mouth opening. There is a band of long cilia on each side of the

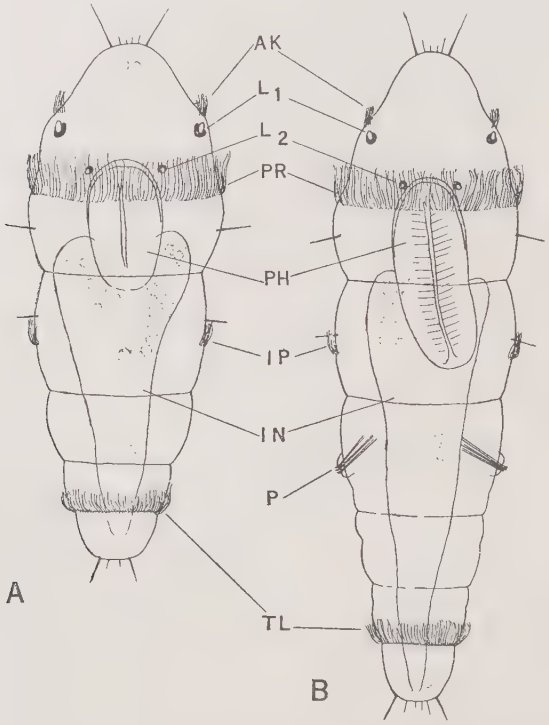

Fig. 2.—Larvæ of *A. pictus*, (A) one-day old and (B) six-day old, from Mr. Wilson's sketches.

AK—akrotroch; L1—anterior pair; L2—posterior pair of eyes; IN—intestine; IP—inter-paratroch; P—parapodium with setæ; PH—pharynx; PR—prototroch; TL—telotroch.

cephalic section in front of the anterior eyes, as in the older larva of *Autolytus longeferiens*. I think that perhaps each band is connected by a row of shorter cilia, and constitutes a complete ring, the akrotroch. The telotroch marks the boundary of the body and the pygidium. The interparatroch is already distinct in the middle of the second section of the body, and not in the third. It is present on the ventral surface only (gastrotroch). There are a number of sensory hairs at both extremities, and also spine-like tactile hairs on each side behind the prototroch, in the

cephalic section and in the middle of the third segment, just in front of the interparatroch. The main portion of the gut consists of an ovoid stomodeal invagination and an intestine, which contains a quantity of yolk. It is important to call attention to the position of the larval pharynx, which is unmistakably within the boundary of the cephalic

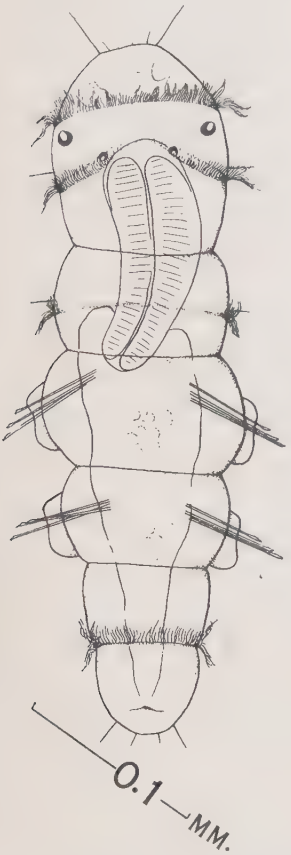

Fig. 3.—6-meric larva of *A. longeferiens*, three-day old, dorsal view.

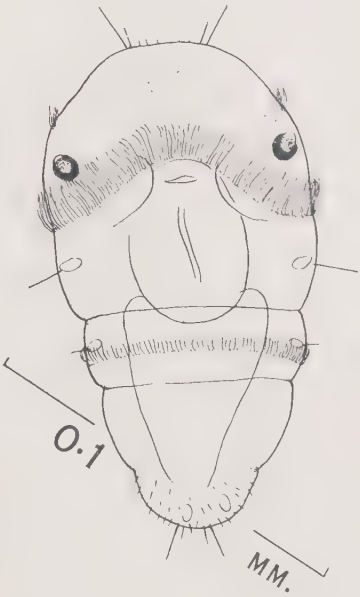

Fig. 4.—3-meric larva of *A. prolifer* (?) just before hatching, ventral view.

section. It scarcely extends into the second segment carrying the interparatroch.

After six days, a mono-setigerous larva (0·3 mm. long) results, to which (Fig. 2B) one more segment is added at the hinder section of the body. There is no change in the front part. The first pair of bundles of setæ is now visible. They are formed in the third section of the larva. But we should not fail to notice that this is next to the segment bearing the

interparatroch, so that it corresponds to the fourth segment of the *A. longeferiens*—larva figured by Mrs. Sexton. There is another consideration to support this view, in addition to the position of the interparatroch. As mentioned above, the stomodeal invagination comes down from the mid-ventral position of the cephalic section, instead of from the band-bearing segment. According to Malaquin (l.c., p. 392), the stomodeal invagination should have already been complete and the mouth open by this stage of development. The cephalic section is in close connection with the stomodeal invagination, and this invagination takes place both theoretically and actually between the epi- and hypo-sphere of the trochophore, and thus it seems not unreasonable to suppose that we are here dealing with a non-segmented condition of the prostomium and the buccal segment, as in the development of Nereis (see E. B. Wilson, 1892, p. 424). The buccal segment must become individualized at a later period of development (see Fig. 5).

I could not actually find a trace of the division into two segments in the cephalic section of the Syllidian larvæ in the early phases of development. The head (Fig. 3) is always completely marked off from the body by a distinct constriction lying immediately in front of the segment bearing the interparatroch. The buccal segment, therefore, constitutes morphologically an integral part of the head in this case, though, of course, it belongs to the first segment of the "Soma."

Before the stage just discussed, the larvæ are without doubt less segmented and without setæ at all. To them are referred the metatrochophores of *Eusyllis assimilis* drawn by Malaquin (see l.c., pl. XIII, fig. 19) and *Odontosyllis ctenostoma* figured by Herpin (see l.c., pl. V, fig. 87). There are two constrictions and three divisions; these are in *Autolytus prolifer* (Fig. 4) the anterior cephalo-buccal section, the median first setegerous segment and the posterior somato-pygidial section. Herpin (l.c., p. 166) describes the development of the 3-meric body of *Odontosyllis ctenostoma* into the condition of seven segments as follows: "La plus jeune larve observée (pl. IV, fig. 87) possède déjà trois couronnes ciliées inegalement développées, dont une cephalique. Bientôt (pl. IV, fig. 88) une quatrième apparaît, en même temps que les segments s'individualisent. Au maximum de développement (pl. IV, fig. 91), les larves pélagiques *d'O. ctenostoma* présentent six forts couronnes ciliées." The larvæ are then 7-meric and bi-setigerous (pl. IV, fig. 92).

According to the known data, it may be stated that those larvæ in which the early developmental stages are most slowly passed through are polytrochal, cilia appearing very early and, except those of the special bands, being confined to the dorsal surface and disappearing from in front backwards. In other larvæ, in which the early stages are abbreviated, the cilia do not appear until a later period, and then only on the

head (akro- and proto-troch) and between the last two segments (telo- or para-troch), (Malaquin, l.c., pp. 389–426, from Gravely, 1909, p. 8) with slight modifications. There is generally an interparatroch (on the ventral surface) in the middle of the future first setigerous segment. The formation of parapodia seems to commence from the second setigerous segment, and not from the first.

The 9-meric stage is followed by the 11-meric stage (Fig. 5). (The number of segments is not very important and larvæ of ten or twelve segments appear as well.) The morphology of the head is near completion, and the stomodeal invagination is divided into a long anterior pharynx proper, and a short posterior proventricular portion. The ventriculus may be differentiated also. According to Herpin (l.c., p. 166) a mono-pharyngeal condition continues, in *Odontosyllis ctenostoma*, until the 13-meric stage, and it is also at this time that the central cirri of the buccal segment are formed. The palpi may appear quite early in *Syllis armillaris* (according to Malaquin at the 7-meric stage) or their appearance is retarded, in *Odontosyllis ctenostoma*, until the 15-meric stage. In any case a juvenile Syllid is complete at the stage of seventeen segments, thirteen being setigerous. The pharynx then reaches the posterior border of the fifth setigerous segment, and the intestine commences from the sixth segment. In Amblyosyllis, the only further development is to specialize the individual metameres, in each portion of the body parts as already determined, the growth zone being directly transformed into the penultimate tetracirrigerous segment. However, Syllids have generally more segments than seventeen, and growth must be continued. This is but a simple repetition of the same segmentation in the hinder section of the body, the manner of which is well known and requires no description in this place.

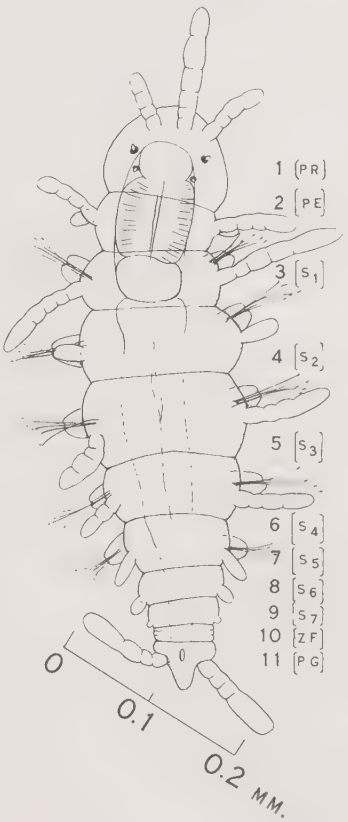

FIG. 5.—11-meric larva of *Syllis* sp. found on the colony of Syncoryne with *Procerastea halleziana*.

1 (PR) prostomium, 2 (PE) peristomium, 3 (S1) first setigerous segment . . . , 10 (ZF) growth zone, 11 (PG) pygidium.

The length of Amblyosyllis is by no means the shortest among Syllids, but perhaps of the smallest number of segments. *A. lineata* (=*Pterosyllis formosa*) as well as *A. speciosa* (a Japanese species described by Izuka, 1912, p. 183) consists almost constantly of seventeen segments, thirteen of which, i.e. from the third to fifteenth, are setigerous. The first segment is, of course, the prostomium, the second the peristomium, and the last the pygidium as usual, but the penultimate segment of this peculiar Syllid is also, as mentioned just above, without parapodia and bears instead two pairs of long cirri like the second segment. Malaquin (l.c., p. 423, pl. XIV, fig. 30) has figured a young " Pterosyllis " of eight segments succeeded by a pygidium; he, however, does not draw any segment without setæ between the last two segments, that is between the eighth setigerous one and the pygidium. It is, therefore, quite problematical in this case whether the penultimate, i.e. the eighth setigerous segment, represents the active zone. Malequin (l.c., p. 291), in another place, in describing the development of the Stolons of Myrianida, lays great weight upon the importance of the pygidium, so far as its first appearance in chain formation is concerned, and Meusch (1900, p. 278) states that a new growth zone which contributes to the elongation of the Stolon, arises in *Autolytus variens* actually from the anal segment and in the course of its development it does not receive any contribution from the setigerous segment preceding it. Such an origin of the growth zone (in stolonisation) is entirely adverse to what I have described so far. Discussion of this problem, however, I shall not enter upon now, but postpone until another occasion, when " the Schizogamy of the Syllidæ " will be particularly considered.

But I should not postpone my acknowledgment to Dr. E. J. Allen, the Director of the Laboratory, and thanking him for help in various ways. Mrs. E. W. Sexton has helped me greatly by her generous permission to copy two larval *Autolytus longeferiens* from her beautiful colour sketches, both shown in Fig. 1, and to Mr. D. P. Wilson I am greatly indebted for two very young stages of *Autolytus pictus* shown in Fig. 2. I thank both for their kind help.

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Gravely, F. H. 1909. Polychæt Larvæ. L.M.B.C. Memoirs. (Perhaps both larvæ figured in pl. I, figs. 1 and 5, judging from the author's drawings, will not belong to those of Syllids.)

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Additions to the Sponge Fauna at Plymouth.

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With 9 Figures in the Text.

During a short visit to Plymouth, in 1928, Dr. M. W. de Laubenfels made a collection of sponges which, with the exception of six, he identified and deposited in the Biological Laboratory at Plymouth. Before leaving England he left these six with me, with the request that they should be identified. This I have now done, and the results have proved extremely interesting, adding six species, *Halichondria bowerbanki*, *Mycale similaris*, *Iophon hyndmani*, *Endectyon delaubenfelsi*, *Hymedesmia stephensi*, and *Pachaxinella subdola*, to the recorded faunal list for Plymouth, of which three are new species.

Halichondria bowerbanki sp. n.

Spongia coalita Lamouroux 1816, p. 80 ; Lamarck 1816, p. 382 ; Grant 1825, pp. 95, 96, 101, 102, 105, 340 ; Id. 1826 *a*, pp. 114, 116–118, 120, 338 ; Id. 1826 *ζ*, p. 347 ; Id. 1826*η*, pp. 123, 135.

Halichondria coalita Fleming 1828, p. 522 ; Bellamy 1839, p. 268 ; Johnston 1842, p. 135, pl. xii, fig. 1 ; Bowerbank 1866, p. 238 ; Parfitt 1868, p. 11.

Amorphina coalita Schmidt 1870, p. 77.

Halichondria coalita Bowerbank 1874, p. 102, pl. xli, figs. 18–20 ; Id. 1882, p. 96.

Halichondria panicea (pars) Levinsen 1887*a*, p. 512.

Amorphina coalita Topsent 1888, p. 146.

Halichondria coalita Topsent 1911*a*, pp. i–xv ; Id. 1913, p. 31.

Diagnosis.—Sponge typically repent, and sub-ramose or profusely branched ; branches frequently anastomosing ; surface smooth, slightly uneven ; texture compact, friable ; oscules small, few, or not apparent ; colour, in life, yellowish, dried, white ; oxea ranging from ·2 by ·003 to ·33 by ·012 mm.

(There is little to choose between this species and *Halichondria panicea*. The main differences are that in *H. bowerbanki* the external form is usually ramose, the oscules are inconspicuous, the dermal reticulation more

strongly marked, and the oxea slightly stouter. Topsent (1911*a*) has also shown a difference in the larvæ of the two species.)

Remarks.—The species *coalita*, usually ascribed to Bowerbank or Johnston, is first mentioned by Müller (1776), but between the date of its inception and the year in which Johnston gave it an adequate description and illustration, its history is a series of errors and confusions. Müller appears to have taken as his type the specimen figured by Ellis (1755, p. 80, pl. xxxii, fig. F ; not p. 95, as quoted by Müller), which is almost certainly a slightly atypical, though fairly common, form of *Chalina oculata*, and to which Ellis gave the name of *Spongia ramosa Britannica*. Thirteen years later Müller (1789) once again refers to *Spongia coalita*, this time giving his own figure, that of a white encrusting sponge growing on a branching Cœlenterate. It is impossible to tell what this sponge was, but it was most probably a specimen of *Halichondria panicea*. Gmelin (1791, p. 3825) described *Spongia coalita* as " Sp. ramosissima mollis tenera flava, ramis compressiusculis. Habitat in mari norwegico." This helps very little, but since Gmelin probably took his ideas from Müller, we may justifiably regard it as a synonym of *Chalina oculata*. In the same way, Bosc (1802, p. 146), in describing the species as " Très-rameuse, molle, tendre, jaune ; les rameaux applatis," was probably following Müller's first description, and we may regard his sponge as *Chalina oculata*. Turton (1806, p. 662) appears to have merely translated Bosc's description when he says, " Very much branched, soft, tender, yellow, the branches a little compressed."

Lamouroux (1816), on the other hand, appears to have had before him a sponge similar to that which Johnston and Bowerbank both figure as *Halichondria coalita*. He says ," base étalée en membrane qui enveloppe plusieurs corps et qui se divise en rameaux prolifères, mous, doux au toucher ; surface irregulièrement réticulée." At the same time, even this is open to doubt. He quotes *Spongia Lycopodium* Esper as a synonym, which is quite wrong. Lamarck (1816), who appears to be slavishly following Lamouroux, even to the extent of quoting *S. Lycopodium* as a synonym, describes *S. coalita* as " Sp. basi dilatata, corpora aliena obvolvens, ramosissima ; ramis tereticompressis, ramulosis ; superficie fibris apressis."

Montagu (1818, p. 80) gives as his diagnosis of *S. coalita*, " much branched in an irregular and distorted manner, rather compressed and of brittle corky substance," a description aptly fitting *Chalina oculata* when dried. Gray (1821, p. 355) in describing his " Coalescent Tuphe," uses almost the same words as Montagu, but treats the sponge as an alga.

Grant, from whose papers Johnston quoted extensively in his description of *Halichondria coalita*, and Fleming (1828, p. 522), were evidently dealing with the sponge Bowerbank (1874) so clearly figured. Fleming gives as

his diagnosis, "growth very irregular, branches more or less compressed, frequently uniting; substance resembling *H. papillaris* (which we now know to be a synonym of *H. panicea*); tubular processes sometimes occur on the sides of the branches, with small round orifices. It grows on dead shells or invests corallines, beyond low-water mark." Bellamy, in recording the sponge from South Devon, merely remarks that it is "not uncommon on exposed beaches." His sponge is, therefore, clearly not *Chalina oculata*, but is probably *Halichondria coalita* or *H. panicea*.

Blainville (1834, p. 532) merely quotes Müller.

After this date, following the accounts given by Johnston and Bowerbank, the conception of *H. coalita* becomes quite clear and consistent.

Prior to Johnston, therefore, we can divide the references to the species into three groups; those probably synonymous with *Chalina oculata*, with *Halichondria panicea*, and with another species which I shall call *H. bowerbanki* sp. n., as follows :—

Chalina oculata.

Spongia coalita Müller 1776, p. 256.
Spongia coalita Gmelin 1791, p. 3825.
Spongia coalita Bosc 1802, p. 146.
Spongia coalita Turton 1806, p. 662.
Spongia coalita Montagu 1818, p. 80.
Tupha coalita Gray 1821, p. 355.
Spongia coalita Blainville 1834, p. 532.

Halichondria panicea.

Spongia coalita Müller 1789, p. 71, pl. 120.
Halichondria coalita Bellamy 1839, p. 268.

Halichondria bowerbanki sp. n. with synonymy as given at the beginning.

Since Bowerbank's specimen is the only one which has survived, and of which we can have first-hand knowledge, I take this for the holotype of the new species.

Distribution.—Arctic Seas; Norway; British Isles; France.

Mycale similaris (Bowerbank).

(See Topsent 1924, p. 109.)

Remarks. I have re-examined the holotype of *Raphiodesma fallaciosum* Bowerbank and find, as Topsent (l.c., p. 84) tentatively suggests, that it is a synonym of *Mycale similaris*.

Distribution.—Jersey; Westport, Ireland; France, North and East coasts.

Iophon hyndmani (Bowerbank).

Remarks.—As I hope shortly to publish a comprehensive study of the Iophoneæ generally, it is inadvisable to say more concerning this species now.

Distribution.—British Isles generally and, probably, along the whole of the Atlantic coast of Europe.

genus **Endectyon** Topsent.

Genotype.—*Phakellia tenax* Schmidt.

Diagnosis.—Ectyoninæ of erect, branching habit; branches supported by an axial skeleton composed of a uni- or multispicular reticulation of smooth styli, which may be partially or wholly replaced by acanthostyli; surface of sponge rendered hispid by projecting brushes of long smooth styli, with which a third category of spicule, slender styli, may be associated.

Endectyon delaubenfelsi sp. n.

(Text figs. 1, 2, 3.)

Holotype.—B.M. 29.8.21.3.

Diagnosis.—Sponge erect, stipitate, branched, composed of a number of irregular branches lying in one plane; surface coarsely hispid; oscules and pores not apparent; colour, in life, golden-yellow; skeleton composed of an axial reticulation of small styli and acanthostyli, which gives off short bundles of spicules on its outer fringes to run vertically to dermis; surface echinated by bundles of long styli; spicules:—(i) long smooth styli, usually straight, almost entirely confined to surface brushes, ·85 by ·007 to ·012 mm.; (ii) short styli, smooth, usually curved, often vermiform, roughly divisible into two categories, ·18 by ·005 mm. and ·225 by ·005 mm.; (iii) acanthostyli, sparingly beset with spines which occasionally form a crown at either base or apex of spicule, ·18 by ·006; microscleres absent.

Remarks.—The species is interesting from many points of view. In the first place, new species of sponges are rarely found in British waters to-day, and it is extremely likely that this one has been overlooked hitherto owing to its extremely close resemblance to *Raspailia ventilabrum* (Bowerbank). Indeed, from external appearance only it is quite impossible to tell the two species apart. This emphasizes, once again, the great need for examining all sponges microscopically in order to be absolutely certain as to their identity.

The present species is the third one recorded for the genus *Endectyon*, the other two, *E. tenax* and *E. demonstrans*, having been found off Florida and the Azores respectively (see Topsent 1920 *β*, pp. 23–26).

The chief interest attaching to it, however, is that the spiculation shows

the manner in which the acanthostyli of the Ectyoninæ may have arisen. The axial skeleton of the branches consists of a multispicular reticulation of triangular meshes, built up of small styli, for the

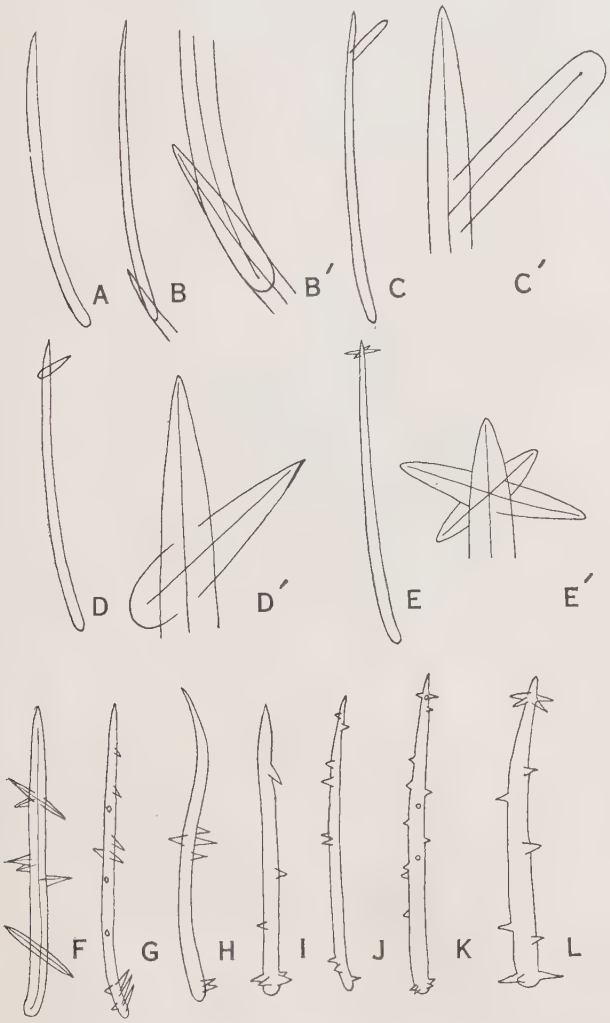

Fig. 1.—*Endectyon delaubenfelsi* sp. n. A. Normal stylus of main skeleton; B–E. abnormal styli (B′–E′. abnormalities enlarged); F–H. abnormal styli showing transitions to normal acanthostyli; I–L. normal acanthostyli. All figures (except B′–E′) × 220.

most part curved, and acanthostyli. The latter, however, are of comparatively rare occurrence. The typical form (figs. 1 I, L.) is that of a smooth style bearing a few stout spines. In a few cases, the

spines have become so grouped that the spicule is ornamented by crowns of spines, four to six in number, at either end of the spicule. In this condition the spicules closely resemble those of the genotype, *E. tenax* (see Topsent, l.c., p. 24, fig. 4b). On the other hand, the smooth styli of the axial skeleton frequently bear abnormal growths, and it is possible to pick out a series of such abnormalities showing a transition which effectually bridges the gulf between the smooth styli and the acanthostyli. In this species, at all events, the acanthostyli have arisen from an abnormal (pathological ?) condition of the styli. The next question, for which as yet there is insufficient evidence to provide an answer,

Fig. 2.—*Endectyon delaubenfelsi* sp. n. × 3/4.

concerns the origin of the acanthostyli of the remainder of the Ectyoninæ, whether they too arose originally as abnormalities and what factors led to their stabilisation.

Endectyon is apparently closely related to *Hemectyon* Topsent (genotype *Raspailia hamata* Schmidt), *Tethyospira* Topsent (genotype *Tethea spinosa* Bowerbank), and, possibly, *Acarnus*.

Distribution.—Plymouth.

KEY TO SPECIES OF ENDECTYON.

1 { Axial skeleton composed exclusively of acanthostyli . . . . . *demonstrans*
  { Axial skeleton composed of a mixture of smooth styli and acanthostyli **2**

2 { Acanthostyli invariably with a crown of recurved spines at each end . . . *tenax*
  { Acanthostyli only occasionally bearing a crown of spines at either end . *delaubenfelsi*

Hymedesmia stephensi sp. n.

(Fig. 4.)

Holotype.—B.M. 29.8.21.5.

Diagnosis.—Sponge thinly encrusting; surface uneven, minutely

hispid, in places slightly conulose ; oscules few, scattered, conspicuous ; pores not apparent ; colour, in life, brown ; texture, in life, " slimy " ; megascleres of main skeleton divided into two categories, long acanthostyli, usually slightly curved, sparingly spined and often quite smooth, ·225 by ·007 mm., and small entirely spined acanthostyli, ·048 by ·002 mm. ; tornota very variable in shape, straight, smooth, with hastate mucronate, strongylote, or slightly tylote heads, ·165 by ·003 mm.

Remarks.—The species finds its closest ally in *H. mucronella* Lundbeck, from which it differs in many important respects, notably in the size and

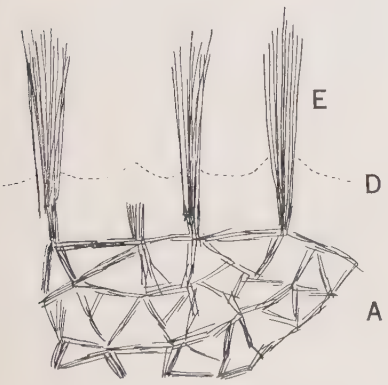

Fig. 3.—*Endectyon delaubenfelsi* sp. n. Section at right angles to surface, showing, A, reticulation of styli and acanthostyli of internal skeleton ; D, dermis ; and E, echinating tufts of long styli at the surface. (Diagrammatic.)

Fig. 4.—*Hymedesmia stephensi* sp. n. A, styli of main skeleton, × 260 ; B, acanthostyle, × 260 ; C, heads of tornota, to show variability in form, × 2600.

shape of the acanthostyli and the variability of the ends of the tornota. The small size of the smaller acanthostyli is, indeed, its characteristic feature.

Dr. de Laubenfels describes this sponge in life as " brown, slimy."

Distribution.—Plymouth.

List of species of Hymedesmia recorded for the British Isles.

The following list of 21 species of *Hymedesmia* represents the complete list recorded for the British Isles. So far, the only species recorded for the Plymouth area is *H. stephensi* sp. n., but since there is no obvious reason why they may not all be found there, in time, I have

thought it worth while to give this list. Several of the British species described by Bowerbank have hitherto been only inadequately described. The re-descriptions given here are based on a re-examination of the types.

GENUS **HYMEDESMIA** Bowerbank.

Genotype.—*H. zetlandica* Bowerbank.

Diagnosis.—Ectyoninæ of encrusting habit; main skeleton composed of acanthostyli, of one or more kinds, variable in size, placed vertically with their bases echinating the substratum; dermal skeleton composed of tornota variously disposed, either in bundles running vertically from the apices of the acanthostyli to the surface, in scattered bundles, or in a horizontal layer supporting the dermis; microscleres chelæ, occasionally absent, and/or sigmata.

1. H. ZETLANDICA Bowerbank.

H. zetlandica Bowerbank 1864, p. 190; Id. 1866, p. 152; Gray 1867, p. 537; Id. 1874, p. 73, pl. xxix, figs. 1–7; *Myxilla zetlandica* Vosmaer 1880, p. 126; *Hymedesmia zetlandica* Bowerbank 1882, p. 70; Topsent 1888, p. 142; *Leptosia zetlandica* Id. 1894, p. 31; *Hymedesmia zetlandica* Stephens 1921, p. 32, pl. iv, fig. 3.

Distribution.—Shetland Is.; S.W. coast of Ireland.

2. H. RADIATA Bowerbank.

H. radiata Bowerbank 1866, p. 149; *Epicles radiatus* Gray 1867, p. 521; *Hymedesmia radiata* Bowerbank 1874, p. 71, pl. xxviii, figs. 1–4, pl. xxix, fig. 8; Id. 1882, p. 56; *Myxilla radiata* Topsent 1892, p. 109; *Hymeraphia radiata* Hanitsch 1894, p. 196; Dendy 1921, 84.

Diagnosis.—Megascleres of main skeleton divided into two categories, long, smooth styli, usually straight or nearly so, sometimes slightly subtylostylote, up to 1·8 by ·012 mm., and entirely spined acanthostyli, with somewhat pronounced head, from ·075 by ·004 to ·24 by ·009 mm.; tornota, sometimes inclined to be slightly vermiform, arranged for most part in stellate groups in dermis, with strongylote ends, ·27 by ·003 mm.

Remarks.—The specimen described by Dendy under this name evidently represents a totally different species which I propose to call *Hymedesmia dendyi* sp. n. The suggestion made by Dendy, that Topsent's *Myxilla radiata* differs specifically from *Hymedesmia radiata*, is almost certainly wrong.

Distribution.—Shetland Is., and the Minch, Scotland; Azores.

3. H. PAUPERTAS (Bowerbank).

Hymeniacidon paupertas Bowerbank 1866, p. 223 ; Id. 1874, p. 93, pl. xxxvii, figs. 4–8 ; *Myxilla paupertas* Vosmaer 1880, p. 127 ; *Hymeniacidon paupertas* Bowerbank 1882, p. 92 ; *Myxilla paupertas* Ridley and Dendy 1887, p. 143 ; *Hymeraphia paupertas* Hanitsch 1894, p. 177 ; Topsent 1894 *β*, p. 18 ; *Hymedesmia paupertas* Stephens 1912, p. 28 ; Id. 1921, p. 31, pl. iv, fig. 1.

Remarks.—Contrary to the assertion of Ridley and Dendy (l.c.), Bowerbank's preparations show that the species is, quite unmistakably, a *Hymedesmia*. *Myxilla paupertas* Topsent (1904, p. 168) is obviously different to Bowerbank's species and, since it is almost certainly a true *Myxilla*, I propose for it the name *M. topsenti* sp. n.

Distribution.—Greenland ; Shetland Is. ; W. and S.W. coasts of Ireland.

4. H. BRONDSTEDI sp. n.

Hymeniacidon dujardinii Bowerbank 1866, p. 224 ; Id. 1874, p. 95, pl. xxxviii, figs. 1–4 ; Id. 1882, p. 92 ; *Stylopus dujardini* Levinsen 1887*a*, p. 512 ; *Dendoryx dujardini* Topsent 1888, p. 146 ; Id. 1890, p. 201 ; Id. 1891, p. 528 ; Id. 1892, p. 99 ; *Myxilla radiata* Id. l.c., p. 109 ; *Leptosia dujardini* Id. 1894*a*, p. 37 ; Id. 1896 *β*, p. 275 ; Id. 1902 *β*, p. 353 ; Id. 1904*a*, p. 185, pl. i, fig. 5 ; *Hymedesmia dujardinii* Lundbeck 1909, p. 444 ; Id. 1910, p. 101, pl. x, fig. 5 ; *Hymedesmia dujardini* Arndt 1912, p. 119 ; Stephens 1917, p. 11 ; Id. 1921, p. 40.

Remarks.—In describing his *Hymeniacidon dujardinii*, Bowerbank was under the impression that it was specifically identical with Johnson's *Halisarca dujardinii*. Since this is clearly a case of wrong identification, the name *dujardinii* as applied to *Hymeniacidon* and, since Bowerbank's time, to *Hymedesmia*, cannot stand. I propose, therefore, the name *brondstedi*.

Distribution.—N.E., S.E., and W. coasts of Ireland ; Greenland ; Norway.

5. H. OCCULTA Bowerbank.

H. occulta Bowerbank [in] Norman 1869*a*, p. 331 ; Id. 1874, p. 250, pl. lxxix, figs. 9–11 ; *Myxilla occulta* Vosmaer 1880, p. 129 ; *Hymedesmia occulta* Bowerbank 1882, p. 56 ; *Desmacidon occultum* Hanitsch 1894, p. 180 ; *Hymeraphia occulta* Topsent 1894 *β*, p. 12 ; *Leptosia occulta* Id. 1904*a*, p. 186, pl. xv, fig. 1 ; *Hymedesmia occulta* Lundbeck 1910, p. 67, pl. iii, fig. 6, pl. vii, fig. 8 ; Stephens 1921, p. 37.

Distribution.—Greenland ; Shetland Is. ; W. and S.W. coast of Ireland ; Azores.

6. H. CRUX (Schmidt).

Desmacidon crux Schmidt 1875, p. 118, pl. i, figs. 10–11 ; *Hymedesmia crux* Thiele 1903*a*, p. 392, pl. xxi, fig. 26 ; Lundbeck 1910, p. 83, pl. iii, fig. 11, pl. viii, fig. 10 ; Stephens 1921, p. 38.

Distribution.—Greenland ; Norway ; Faröes ; S.W. coast of Ireland.

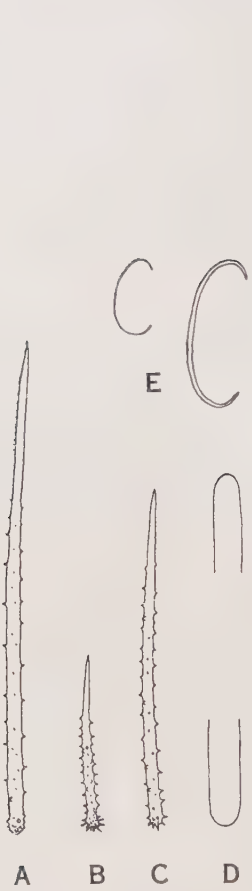

FIG. 5.—*Hymedesmia pilata* Bowerbank. A–C, acanthostyli, showing three typical sizes, × 260 ; D, ends of a typical tornote, × 2600 ; E, sigmata, × 650.

FIG. 6.—*Hymedesmia peachii* Bowerbank. A–C, acanthostyli of main skeleton, × 260 ; D, ends of tornota, × 2600 ; E, isochela arcuata, × 1300.

7. H. PANSA Bowerbank.

H. pansa Bowerbank 1882, p. 56, pl. i, figs. 1–4 ; *H. pulchella* Id. l.c., p. 61, pl. ii, figs. 5–8 ; *H. pansa* Stephens 1912, p. 29 ; Id. 1917, p. 11 ; Id. 1921, p. 36, pl. iv, fig. 4.

Remarks.—*H. pulchella* differs from *H. pansa* in the smaller size of its spicules only. The following are the maximum dimensions of the spicules of *H. pulchella* : large acanthostyli, ·22 by ·006 mm. ; small acanthostyli, ·09 by ·007 mm. ; tornota, ·18 by ·003 mm. ; isochelæ, ·019 mm.

Distribution.—W. coast of Ireland ; Roscoff, France (*fide* Stephens 1912, p. 300).

8. H. PILATA Bowerbank. (Fig. 5.)

H. pilata Bowerbank 1882, p. 59, pl. ii, figs. 1–4.

Diagnosis.—Acanthostyli not divisible into two categories, spined for the greater part of length but smooth in distal portion, spining particularly pronounced at base, varying from ·078 by ·009 to ·24 by ·008 mm., including spines ; tornota extremely slender, straight, with strongylote ends, ·12 by ·0015 mm. ; microscleres sigmata of two sorts, ·015 and ·03 mm. long respectively.

Distribution.—Birterbuy Bay, W. coast of Ireland.

9. H. PEACHII Bowerbank. (Fig. 6.)

H. peachii Bowerbank 1882, p. 64, pl. xiii, figs. 5–12.

Diagnosis.—Acanthostyli not divisible into two categories, spined for greater part of length but smooth in distal portion, spining particularly strong near base, varying from ·105 by ·012 to ·39 by ·022 mm., including spines ; tornota slender, straight, with bluntly oxeote ends, ·195 by ·003 mm. ; isochelæ arcuatæ, ·03 mm. long.

Remarks.—The chelæ vary considerably in shape. The one figured probably represents the typical form, but large numbers may be found in which the shaft is more strongly curved.

Distribution.—Wick, North Britain.

10. H. ARMIGER (Bowerbank).

Hymeniacidon armiger Bowerbank 1882, p. 73, pl. iv, figs. 10–17.

Remarks.—The species undoubtedly belongs to Hymedesmia and Bowerbank's figures show this clearly. The reason for its having been so long ignored is probably to be found in the fact that his figures are misleading in regard to the size of the spicules. The megascleres are faithfully portrayed, the acanthostyli measuring from ·075 to ·22 mm. in length, and the tornota ·175 by ·003 mm. The microscleres are chelæ arcuatæ, chiefly remarkable for their small size, ·012 mm. long, and form the characteristic feature of the species.

Distribution.—Roundstone Bay, Ireland.

11. H. KŒHLERI (Topsent).

Leptosia kœhleri Topsent 1896*β*, p. 284, pl. viii, figs. 7–9 ; Id. 1904*α*, p. 188 ; Lundbeck 1910, p. 42, pl. v, fig. 5 ; Stephens 1921, p. 34.

Distribution.—Greenland ; Iceland ; Faröes ; W. and S.W. coasts of Ireland ; Bay of Biscay ; Azores.

12. H. MUCRONATA (Topsent).

Hymeraphia mucronata Topsent 1904*α*, p. 165, pl. xiv, fig. 4 ; *Hymedesmia mucronata* Lundbeck 1910, p. 98, pl. x, fig. 3 ; Stephens 1921, p. 39.

Distribution.—Greenland ; S.W. coast of Ireland ; Azores.

13. H. MUTABILIS (Topsent).

Hymeraphia mutabilis Topsent 1904*α*, p. 166, pl. xiv, fig. 3 ; *Hymedesmia mutabilis* Stephens 1921, p. 38.

Distribution.—S.W. coast of Ireland ; Azores.

14. H. BACULIFERA (Topsent).

H. baculifera Topsent 1902*β*, p. 354 ; Id. 1904*α*, p. 191, pl. xv, fig. 2 ; Lundbeck 1910, p. 71, pl. viii, fig. 1 ; Stephens 1915*α*, p. 440 ; Id. 1921, p. 37.

Distribution.—Greenland ; Iceland ; Faröes ; S.W. Ireland ; Mediterranean coast of Algeria ; Azores ; Saldanha Bay, S. Africa.

15. H. CURVICHELA Lundbeck.

H. curvichela Lundbeck 1910, p. 48, pl. vi, fig. 2 ; Stephens 1921, p. 34.

Distribution.—Greenland ; S.W. coast of Ireland.

16. H. TRUNCATA Lundbeck.

H. truncata Lundbeck 1910, p. 77, pl. iii, fig. 9, pl. viii, fig. 6 ; Stephens 1921, p. 33.

Distribution.—Greenland ; Iceland ; Faröes ; S.W. coast of Ireland.

17. H. DIGITATA Lundbeck.

H. digitata Lundbeck 1910, p. 90, pl. iii, fig. 15, pl. ix, fig. 4 ; Stephens 1921, p. 39.

Distribution.—Greenland ; S.W. coast of Ireland.

18. H. TENUISIGMA Lundbeck.

H. tenuisigma Lundbeck 1910, p. 100, pl. x, fig. 4 ; Stephens 1921, p. 39.

Distribution.—Greenland ; W. coast of Ireland.

19. H. HELGÆ Stephens.

H. helgæ Stephens 1915, p. 236 ; Id. 1921, p. 40, pl. iv, fig. 6.
Distribution.—S.W. coast of Ireland.

20. H. SPINOSA Stephens.

H. spinosa Stephens 1916, p. 237 ; Id. 1921, p. 41, pl. iv, fig. 5.
Distribution.—S.W. coast of Ireland.

21. H. HIBERNICA Stephens.

H. hibernica Stephens 1916, p. 237 ; Id. 1921, p. 42, pl. iv, fig. 2.
Distribution.—S.W. coast of Ireland.

22. H. STEPHENSI sp. n.

Distribution.—Plymouth.

KEY TO BRITISH SPECIES OF HYMEDESMIA.

1	With spicules of main skeleton divided into two categories, long, usually basally-spined, and short, entirely-spined, acanthostyli	2
	With spicules of main skeleton of one sort only, but of varying size and, usually, entirely-spined	12
2	With larger spicules of main skeleton spined for some part of length	3
	With larger spicules of main skeleton entirely smooth styli	*radiata*
3	With microscleres	5
	Without microscleres	4
4	With smaller acanthostyli never less than one-third the length of larger acanthostyli	*hibernica*
	With smaller acanthostyli less than one-fifth of larger acanthostyli	*stephensi*
5	Microscleres sigmata only	6
	Microscleres chelæ to which sigmata may be added	7
6	With microscleres less than ·04 mm. long	*pilata*
	With microscleres more than ·04 mm. long	*tenuisigma*
7	Microscleres ancoræ spatuliferæ and sigmata	*mutabilis*
	Microscleres chelæ arcuatæ	8
8	With sigmata	*digitata*
	Without sigmata	9
9	With larger megascleres of main skeleton spined throughout length, strongly in lower, feebly along distal portion	*helgæ*
	With larger megascleres of main skeleton spined in basal portion only	10
10	With chelæ less than ·025 mm. long	*pansa*
	With chelæ more than ·025 mm. long	11
11	With oxeote tornota	*occulta*
	With strongylote, to slightly tylote, tornota	*paupertas*
12	With microscleres	13
	Without microscleres	*brondstedi*
13	Microscleres chelæ and sigmata	14
	Microscleres chelæ only	15
14	With chelæ of one sort only	*zetlandica*
	With chelæ of two sorts	*mucronata*
15	With shaft of chelæ smooth	16
	With shaft of chelæ spined	*crux*

16	With strongylote tornota	17
	With oxeote tornota	19
	With tylote tornota	*truncata*
17	With polytylote tornota	18
	With simple tornota, not polytylote	*baculifera*
18	With shaft of chelæ strongly curved and teeth small	*curvichela*
	With chelæ of normal shape	*kœhleri*
19	With chelæ more than ·02 mm. long	20
	With chelæ less than ·02 mm. long	*armiger*
20	With all acanthostyli strongly and entirely spined	*spinosa*
	With larger acanthostyli smooth in distal half	*peachii*

British Species of Hymedesmia now Removed to Other Genera.

H. stellata Bowerbank 1866, p. 150=*Timea stellata*.

H. simplicima Id. 1874, p. 253, pl. lxxx, fig. 1=*Pseudosuberites simplicima*.

The skeleton of *Hymedesmia simplicima* is composed of tylostyles (fig. 7) only disposed with no apparent order. They measure, on an

Fig. 7.—*Hymedesmia simplicima* Bowerbank. Head of a tylostyle, × 250.

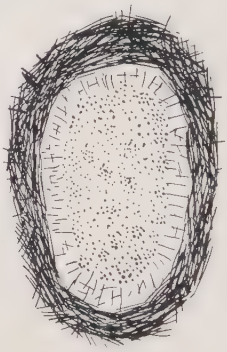

Fig. 8.—*Pachaxinella subdola* Bowerbank. Transverse section of a branch, showing internal axial skeleton of longitudinally-disposed spicules and outer, dermal layer. (Diagrammatic.)

average, ·6 by ·009 mm. The sponge itself is so small that it is difficult to be certain of its systematic position, but it is extremely possible that it is nothing more than the immediate post-fixation stage of a species of *Pseudosuberites*.

H. inflata Id. 1874, p. 245, pl. lxxix, figs. 5–8=*Crella inflata*.

The spiculation of this species consists of acanthoxea, ·096–·12 by ·006 mm., and long, slender tornota, measuring, on an average, ·5 by ·003 mm. The acanthoxea are for the most part slightly curved or sharply angulated and, usually, centrotylote. The tornota have oxeote ends and

are quite straight and smooth. The species closely resembles *C. carnosa* (Topsent), but differs from it in the dimensions of the spicules, the centrotylote character of the acanthoxea, and the absence of polytylote markings on the tornota.

H. acuto-stellata Hanitsch 1894, p. 203.

The original description of this species is quite inadequate, but, so far as one may judge, it is probably an encrusting form, perhaps even the immediate post-fixation stage, of *Dictyocylindrus stuposus*. It is certainly not a *Hymedesmia*.

GENUS **Pachaxinella** gen. n.

Genotype.—Halichondria subdola Bowerbank.

Diagnosis.—Axinellidæ of erect, branching habit; skeleton composed

Fig. 9.—*Pachaxinella subdola* Bowerbank. × 3/4.

of an axial core of loose bundles of spicules surrounded by a dense layer in which spicules are irregularly disposed, sometimes at right angles, sometimes tangential to the surface; spicules smooth styli of varying size.

Remarks.—The genus is closely allied to *Homaxinella*, but differs from it in the arrangement of the skeleton. The usual order of the Axinellidæ, with a dense axial skeleton and a diffuse extra-axial skeleton, is reversed.

Pachaxinella subdola (Bowerbank).

(Figs. 8, 9.)

Holotype.—B.M.—29.11.27.1.

Halichondria subdola Bowerbank 1866, p. 247; Id. 1874, p. 106, pl. xliii, figs. 14–16.

Diagnosis.—Sponge erect, copiously branched, stipitate; surface even, minutely hispid; oscules and pores not apparent; texture firm, brittle when dry; colour, in dried state, creamy-white, alive golden-yellow; axial skeleton composed of loose bundles of spicules running longitudinally through branches, united by moderate quantity of spongin; extra-axial skeleton a dense layer of spicules, very irregularly arranged, sometimes horizontal to surface, sometimes at right angles to it, with all positions between these two; spicules smooth styli, usually straight, varying in size, ·22 by ·003 to ·51 by ·006 mm.

Remarks.—The present specimen, a complete sponge, is practically identical in all essential features with Bowerbank's fragmentary holotype.

The junction between the axial and extra-axial skeletons is marked by a thin, almost imperceptible, zone of loose tissue supported by spicules which emerge from the axial skeleton, almost at right angles to it, and project into the extra-axial zone.

Previously known distribution.—Guernsey.

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The Photo-chemical and Photo-electric Measurement of Submarine Illumination.

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Accounts have been given in previous papers (1925, 1926, 1928) of measurements of submarine illumination carried out near Plymouth by means of photo-electric cells. A further paper (1929, 3) recorded the results so obtained during 1928. An account is now given of photo-chemical measurements made in that year, simultaneously with the photo-electric measurements.

Adaptation of the Uranyl Oxalate Method for Submarine Measurements.

We have elsewhere (1929, 5) described the use, in daylight photometry, of a 0·1 N solution of oxalic acid approximately 0·01 M with respect to uranyl sulphate $UO_2SO_4 \cdot 3H_2O$. The concentration of uranyl sulphate actually used was 4·27 g. per litre, following the practice of other workers, but the rate of decomposition of oxalic acid is independent of the concentration of uranyl sulphate within fairly wide limits.

After exposure of the solution in quartz, or glass, test tubes the oxalic acid remaining was titrated with potassium permanganate. As the amounts used in the deeper submarine measurements were very small, it was necessary to titrate with the greatest care, and an allowance was made colorimetrically for any excess of permanganate added in the final drop.

It was especially desired to obtain information concerning the penetration of the ultra-violet portion of the spectrum. Uranyl oxalate is sensitive to this region, and also to the violet and blue of the visible spectrum, but the sensitivity decreases as the wave-length increases. Quartz tubes were used so that the full effect of the shorter waves should be registered, but the decomposition in both air and water is mainly due to the visible rays and to the glass-passing portion of the ultra-violet. Using tubes of quartz and of Monax resistance glass suspended vertically in air, it

was found that the rate of reaction was 1·14 times as great in the former as in the latter. In other words, only one-eighth part of the decomposition was due to the ultra-violet cut out by the glass. This is very nearly a measure of the portion which is physiologically active in producing erythema, and in activating ergosterol, as explained elsewhere (1929, 6).

Since the decomposition results in the liberation of gas, the rubber corks inserted in the tubes were, at first, provided with narrow glass tubes closed by rubber tubing with a small slit and terminating in a piece of glass rod. The arrangement permits of the escape of gas, while the pressure of the water effects a seal by causing the walls of the rubber tubing to collapse. It was found, however, that the valves often leaked, and, since the rate of decomposition is much reduced under water, the method adopted in all the measurements recorded here was to secure the stoppers with copper wire. The tubes were then attached by copper wire to a weighted line marked in metres. Care was taken to avoid exposing the tubes before they were lowered, and, on hauling up, the wires were snipped and the tubes placed in a light-tight box.

So far as we are aware there is no evidence that the small excess pressure due to the decomposition products in any way affects the rate of reaction ; in other words, it is not a reversible reaction.

Marshall and Orr (1928) state, however, that " there are two objections to the use of the method in the sea. As decomposition goes on, gases are evolved, causing an increase in pressure which inhibits the reaction, and in addition there is superimposed the pressure of the column of sea-water overlying the tube. In the second place absorption of light of very short wave-length by sea-water is rapid, and the results obtained below the surface are low." No experimental evidence is adduced for the statement that the excess pressure (of carbon monoxide and carbon dioxide) inhibits the reaction, which implies that the exertion of pressure upon these gases results in the synthesis of oxalic acid in the presence of water and uranyl sulphate under the action of light. The pressure of the column of sea-water is immaterial, being entirely supported by the walls of the tube and stopper. It remains to be proved that light of short wave-length is rapidly absorbed.

A possible error due to the shading of the tubes by the ship was avoided by attaching the end of the line, to which the tubes had been tied, to the middle of a spar with cork floats at each end. This was then lowered into the sea, and the ship drifted away from it to the full length of the rope, about 20 metres. This method could not be used with the photo-electric photometers owing to their weight. Thus the latter readings are somewhat reduced by shading, though, owing to the precautions taken to lessen this as much as possible, the effect is not important.

Aerial and Submarine Rates of Decomposition.

For comparison with the tubes lowered into the water, similar tubes, each with 10 c.c. of the reaction mixture, were suspended from the topping lift running from the mizen-mast to the end of the boom. These were uncorked, and swung about a mean vertical position, so that they registered the effect of horizontal light. The tubes lowered into the water also took up a vertical position in a flat calm, when there was no drift. Their angle with the vertical became greater and greater the faster the drift, so that no real comparison could be made between the submarine and aerial rates of decomposition. Table I shows the rates in air and in water. The former may be seen to be from about two up to nearly four times as great as the rates at one metre depth, but no exact comparison is permissible owing to changes in the angular distribution of the light in passing through the water surface, and to the reduction in reflection losses at the surface of the tube when immersed.

TABLE I.

Decomposition of Uranyl Oxalate Solutions, 0·1 N with Respect to Oxalic Acid, Exposed in Closed Quartz Tubes 13×1·3 cm. (Internal Diameter) and Lowered in the Sea to the Depths Shown.

The angle with the horizontal varied according to rate of drift of the ship. Work at Station EI, bottom at 72 m.

RATES OF DECOMPOSITION IN C.C. OF 0·1 N OXALIC ACID PER HOUR.

m.	July 11	July 23	Aug. 9	Aug. 29	Sept. 18	Sept. 18	Oct. 2	Nov. 30
0 (air)	10·22	10·67	5·46	9·72	7·31	5·91*	8·07	0·98
1	4·03	4·83	1·51	3·57	1·94	1·87	2·17	0·42
5	2·26	3·38	0·67	2·11	1·43	1·44	1·12	0·21
10	1·29	2·05	0·24	1·09	0·80	0·875	0·54	0·12
15	0·69	1·07	0·103	0·39	0·45	0·53	0·25	0·055
20	—	0·34	0·027	—	0·28	0·365	—	—
25	—	—	0·020	—	0·15	—	—	—
40	—	—	0·000	—	0·095	—	—	—
Exposure, minutes	120	92	180	93	114	114	136	130

PERCENTAGE RATES OF DECOMPOSITION.

m.								
1	100·0	100·0	100·0	100·0	100·0	100*	100·0	100·0
5	56·1	70·0	44·4	59·1	73·8	77·1	51·7	50·0
10	32·4	42·5	15·9	30·5	41·2	46·8	24·9	28·6
15	17·1	22·2	6·8	10·9	23·2	28·4	11·5	13·0
20	—	7·0	1·8	—	14·4	19·5	—	—
25	—	—	1·3	—	7·7	—	—	—
40	—	—	—	—	4·9	—	—	—

* In Monax resistance glass tubes of approximately the same dimensions as the quartz tubes. In air on this date rate in quartz tube was 1·24 times that in glass tube at time of experiment. Asterisk refers to all depths.

At 1 m. the rate varies from 30·4 to 2·65 mg. of crystalline oxalic acid decomposed per hour. The values are, however, recorded in cubic centimetres rather than in milligrams, as this enables the degree of accuracy of the titration to be judged better. The second column for September 18 contains the results obtained using glass tubes instead of quartz. In air and at 1 m. the rates in quartz exceed those in glass, at 5 m. the two are equal, and beyond that the rate for glass is the greater. The values in quartz in air are naturally the greater, since the effect of the shorter waves is added on, but as the proportion of shorter waves becomes reduced, this effect diminishes. The fact that the glass tube rates become the greater below 5 m. can only be attributed to a difference in the angle at which the tubes were riding owing to the unequal weights in water of the closed tubes, the quartz being the greater.

TABLE II.

UNDER C AND E ARE TABULATED THE ABSORPTION COEFFICIENTS, μ_v, CALCULATED ON THE ACTUAL MEAN DEPTHS, AS DETERMINED PHOTO-CHEMICALLY BY URANYL OXALATE AND BY VACUUM AND GAS-FILLED POTASSIUM PHOTO-ELECTRIC CELLS. UNDER C M ARE SHOWN VALUES OF μ_v OBTAINED USING MONAX RESISTANCE GLASS TUBES INSTEAD OF QUARTZ.

	July 11		July 23		August 9		August 29	
m.	C	E	C	E	C	E	C	E
5	0·125	0·101*	0·095	0·075*	0·204	0·183*	0·132	0·123*
10	0·129	0·100	0·115	0·083	0·187	0·181	0·169	0·107
15	—	—	0·180	0·109	0·217	0·192	—	—
20	—	—	—	—	0·165	0·178	—	—
C/E	1·26	—	1·46†	—	1·05	—	1·31	—

	September 18			October 2		November 30	
m.	C	E	CM	C	E	C	E
5	0·098	0·086*	0·084	0·154	0·166*	0·139	0·156*
10	0·116	0·076	0·100	0·150	0·129	0·134	0·125
15	0·105	0·084	0·087	—	—	—	—
20	0·110	0·092	—	—	—	—	—
C/E	1·37	—	1·10‡	1·02	—	0·97	—

* Taking surface losses as 15 per cent.
† Or 1·33 excluding probably erroneous value for 15 m.
‡ CM/E.
Note.—Mean value of C/E = 1·21, and CM/E = 1·10.

In Table II are shown the values of the vertical absorption coefficient, μ_v, calculated as usual from $\mu_v = \frac{2{\cdot}3}{\delta}(\log_{10}p_1 - \log_{10}p_2)$ where δ is the difference in depth and p_1 and p_2 the percentages of the light at the two

depths, as given in Table I ; the depths shown are the mean depths for the values there recorded. Beside the photo-chemically determined (C) values of μ_v, those obtained photo-electrically (E) are tabulated; the values of the latter are the mean of two series, made with photometers L and K while the tubes were being exposed, for the first four dates, and are the values obtained with photometers L, K, and J, respectively, for the final three. As previously shown (1928), L has its maximum sensitivity at 4000 Å.U. and K at 4400 Å.U. J, being also a potassium gas-filled photometer, probably resembles K.

Taking the mean of the same number of values of μ_v, determined by each method, over approximately the same depth, it may be seen that the ratio C/E varies from 0·97–1·46, mean of seven series 1·21. Using glass tubes the ratio is 1·10. We may conclude that the photo-electric measurements and the photo-chemical in glass tubes cover approximately the same spectral region, viz. 4800 Å.U. to 3400 Å.U., so that they measure substantially the same degree of absorption and scattering by the water. The quartz tubes, however, permit of the passage of the shortest wavelengths found in sunlight reaching the earth, namely, down to about 3000 Å.U. The scattering of these shorter waves by the water must be considerably greater than that of the longer. In the air their relative activities are 14 : 100, as deduced from the quartz to glass ratio 1·14. In water, however, the shortest waves are cut out more rapidly than the longer ones, as shown by the higher value of the absorption coefficient, which may be regarded as compounded of the coefficients for the portion that passes glass and for the portion that is stopped by glass.

SUMMARY.

1. The uranyl oxalate method of daylight photometry has been used to determine the absorption coefficient of water at depths down to 40 metres at International Hydrographic Station E1, about 10 miles S.W. of the Eddystone in the English Channel off Plymouth. Using quartz tubes on seven days from July to November inclusive the absorption coefficient varied 0·095 for 5 m. on July 23rd to 0·217 for 15 m. on August 9th ; no seasonal variation was shown. The interpretation of the coefficients has been discussed in the paper dealing with the photo-electric measurements.

2. The ratio of the photo-chemically determined coefficients (using quartz tubes) to the photo-electrically determined values (obtained with potassium vacuum and gas-filled glass cells) varied from 1·02 to 1·46 or to 1·37, omitting a probably erroneous value from a series. Using glass tubes the same ratio was 1·10. The ratios are based upon mean values for the various depth series.

3. The higher absorption coefficient determined photo-chemically may indicate a greater absorption of the shortest wave-lengths, in which case one would expect the ratio of the coefficients to decrease with depth; of this there is, however, no evidence.

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Seasonal Changes in the Nitrite Content of Sea-Water.

By

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Brandt (1927) has summarised and reviewed our knowledge of the nitrogen compounds existing in sea-water, including nitrites. In general, estimations of nitrite in sea-water have been made colorimetrically, using the Griess-Ilosvay reagent, which has also been used in the present work. Usually the amount of nitrite found, recorded as milligrams of nitrogen per cubic metre, was small. Raben's results have been grouped by Brandt as follows, 0 mg., 48 cases ; under 1 mg., 53 cases ; 1–4 mg., 21 cases ; 5–9 mg., 6 cases. Orr (1926) in the Clyde Area, found from under 1 mg. to about 10 mg. in June 1925, the deeper water having more than the upper layers. Harvey (1926) states that, " in a number of water samples from the English Channel, examined either on board ship or immediately after landing, no definitely detectable traces of nitrites could be found either by the Griess-Ilosvay reagent or with the strychnine reagent without sulphuric acid, except in the case of inshore water subject to pollution. After storage an appreciable quantity of nitrite has been detected in several instances. In water from 830 metres in the Bay of Biscay, preserved with mercuric chloride when collected, and in water at various depths up to 3000 metres, similarly preserved, collected by the R.R.S. *Discovery* some 200 miles west of Portugal, no nitrite could be definitely detected."

It may be added that dilute standard solutions of nitrite lose strength by the production of nitrate from nitrite, so the same process must take place in sea-water on storing, as well as the converse.

As is well known, ammonium salts are converted to nitrites by bacterial action, and the latter is oxidised to nitrate by another micro-organism or by air. It seemed probable, therefore, that when ammonium salts were being converted into nitrite, a considerable amount of nitrite must exist temporarily in the sea. Harvey (1928) showed that at International Hydrographic Station E1 there was a rapid production of nitrate* in early

* The reduced strychnine reagent used by Harvey reacts both with nitrites and nitrates. The values have been referred to as nitrate for brevity, since that is normally the major constituent.

autumn, which accompanies the phosphate regeneration found by the writer to take place at E1 simultaneously. The analyses shown in Table I make it clear that this nitrate production is preceded and accompanied by nitrite production. The nitrite test is easier to carry out than is that for nitrate on account of the difficulty of preparing the reduced strychnine reagent required for the latter. The presence of nitrite, moreover, indicates, in sea-water, that nitrate is being produced. Whereas by the nitrate test alone it would require two consecutive samples to establish this. Furthermore, the absence of nitrite in the deep oceanic samples examined by Harvey shows that nitrification has, in them, run its full course to nitrate. Table I contains analyses for E1, E2 mid-Channel, and E3 off Ushant. The dates of analysis are shown opposite A in the bottom line of the table. The values found for the surface waters, even in the warmest period of the year, show conclusively that there has been no significant error due to storage.

TABLE I

NITRITE NITROGEN AS MG. PER CUBIC METRE AT STATIONS E1, E2, E3 DURING 1928–1929.

	Aug. 16	Aug. 16	Aug. 17	Aug. 29	Sept. 18	Oct. 2	Nov. 30	Jan. 2	Mar. 4	Mar. 26	Mar. 26	Mar. 27
m.	E1	E2	E3	E1	E1	E1	E1	E1	E1	E1	E2	E3
0	0·2	0·2	0·2	0·0	<1	13·3	1·4	3·1	11·0	2·7	4·3	3·2
5	—	—	—	0·0	—	12·8	—	—	—	—	—	—
10	—	0·2	—	0·0	—	—	—	—	—	—	—	—
15	0·2	—	0·2	4·3	<1	—	1·4	—	—	—	—	—
20	0·2	—	0·2	38·9	2·0	—	—	—	—	—	—	—
25	38·3	—	0·2	—	14·6	14·2	—	3·4	—	—	—	—
30	—	—	—	—	13·6		—	—	—	—	—	—
40	—	—	—	28·9	—		—	—	—	—	—	—
50	23·5	—	0·2	—	—	—	—	—	—	—	—	—
60	—	5·6	—	—	—	—	—	—	—	—	—	—
70	31·0	—	—	37·4	16·1	15·6	1·4	3·9	8·9	3·1	—	—
80	*	—	—	*	*	*	*	*	*	*	—	—
85		5·4	—								4·0	—
90		*	—								*	—
100			0·2									—
105			*									3·1
A	20/8	20/8	20/8	30/8	19/9	4/10	1/12	3/1	6/3	28/3	28/3	28/3

* Denotes that the bottom has been reached before the depth indicated.

From the analyses it may be judged that there is a rapid nitrification in the hypothalassa during August at E1, a less rapid production at E2, and very little at E3. The blank estimation with the reagents usually amounted to only 0·1 mg. per m^3. According to Harvey's (1926, 1928) values for nitrate at E3 for July 1925 and 1926, the available supplies had been depleted to a greater extent at E1 than at E3, E2 being intermediate.

In October at E1 nitrite production was rapid, but by November 30th nitrite had almost all been converted, as shown by the small amount found and Harvey's high nitrate values for this season. Following, apparently, a late autumn or early winter plankton outburst, the existence of which is quite in keeping with Harvey's 1926 nitrate figures, we find a prolonged nitrite production in early spring, with a peak early in March.

It remains to be considered to what extent the nitrite values found are affected by the discharge of sewage from Plymouth, 22 miles N.W. of E1, or from the coast generally. Table II shows clearly that such an effect is negligible or non-existent, inasmuch as not even at L1, which is only about 300 metres from a large sewage outfall and less than 500 m. from the main outfall, are values found at all as high as at E1 during August. We may conclude, therefore, that, as in the case of phosphate and nitrate, the nitrite content of E1 is due to the operation of cyclic processes occurring at that spot.

TABLE II.

NITRITE NITROGEN AS MG. PER M.^{3}, IN SURFACE SAMPLES, 1928–1929. STATION L1, BELOW LABORATORY IN PLYMOUTH SOUND; L2, AT BREAKWATER; L3, OFF RAME HEAD; L4, HALF-WAY TO EDDYSTONE; L5, AT EDDYSTONE; L6, 5 MILES S.W. OF EDDYSTONE, VIZ. MIDWAY BETWEEN L5 AND E1.

Station.	Sept. 18.	Nov. 30.	Jan. 2.	Mar. 1.	Mar. 26.
L1	3·1	6·0	9·5	9·1	4·8
L2	3·0	3·9	9·5	7·2	—
L3	3·5	3·3	9·2	6·0	3·4
L4	0·0	3·3	7·7	7·9	—
L5	1·0	—	5·6	7·3	—
L6	0·0	1·3	3·5	9·1	—
E1	0·0	1·4	3·1	11·0	2·7
A	19/9	1/12	3/1	6/3	28/3

SUMMARY.

1. The nitrite content of sea-water is a useful indication of the rapid transformation of ammonium salts into nitrates.

2. In August the upper 20 m. of water at Station E1, in the English Channel, were devoid of nitrite, from 0·0 to 0·2 mg. of nitrite nitrogen per m.^{3} being found. At and below 25 m. as much as 38 mg. per m.^{3} was found; off Ushant, at E3, the whole water column was devoid of nitrite.

3. In October at E1 the whole water column contained about 14 mg. per m.^{3}, which had fallen to 1·4 mg. by the end of November. From January to March from 3–11 mg. per m.^{3} was found at E1, and at E3 on March 27th 3 mg. was recorded for the whole isothermal water column.

4. The values given for nitrite nitrogen are unaffected by transport from the shore, since inshore waters and even Plymouth Sound are poorer in nitrite than the lower layers at E1 in August, and the shore effect ceases to be appreciable beyond the Eddystone Lighthouse at the most, usually nearer shore.

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Apparatus for Rapid Electrometric Titration.

By

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With 4 Figures in the Text.

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I. Introduction.

This apparatus was assembled at Millport for the electrometric titration of solutions which, being highly coloured, cannot well be titrated with an indicator. It may be used also for highly dilute solutions, unless they are so slightly buffered that their pH value is appreciably changed by the addition of a small quantity of quinhydrone. Measurement of hydrogen-ion concentrations at the quinhydrone electrode has also been attempted with the apparatus. The apparatus is suitable for use at sea.

II. Outline of a Titration Method.

Biilmann (**1**) has described a method of measuring hydrogen-ion concentrations at what he terms the quinhydrone electrode. Quinhydrone may be considered as an equimolecular compound of quinone, $C_6H_4O_2$, and hydroquinone, $C_6H_4O_2H_2$. In acid aqueous solution there is an equilibrium which may be represented by :—

$$\left[H_2\right] \rightleftarrows K_1 \frac{[C_6H_4O_2]}{[C_6H_4O_2H_2]}$$

(It is necessary to specify that the solution shall be acid, because in solutions with a pH value of 8·0 or more, weak acids are formed by oxidation.)

The square brackets denote molar concentrations ; and in this case of

an equimolecular compound, the concentrations of quinone and of hydroquinone must always be equal, so that there is, in the solution, a concentration of free hydrogen, equal to the constant, K_1. The half-cell formed by the immersion of a gold or platinum electrode in the solution, alters its potential with the hydrogen-ion concentration exactly as does the "hydrogen electrode" half-cell, and may therefore be used for the

TABLE I.

Alkali added. (c.c.)	E.M.F. (m.v.)	Increment of E.M.F.	dE/dx.
0	−64		
		5	0·5
10·0	−59		
		7	1·4
15·0	−52		
		14	3·5
19·0	−38		
		19	6·3
22·0	−19		
		11	11
23·0	− 8		
		19	19
24·0	+11		
		16	40
24·4	+27		
		10	50
24·6	+37		
		6	60
24·7	+43		
		11	110
24·8	+54		
		15	150
24·9	+69		
		45	450
25·0	+114		
		134	**1340**
25·1	+248		
		62	620
25·2	+310		
		32	320
25·3	+342		
		14	140
25·4	+356		

measurement of hydrogen-ion concentrations. It is connected to a standard half-cell (usually a calomel half-cell) by an electrically conducting " bridge " of potassium chloride and agar-agar, and the E.M.F. of the complete cell is measured with a potentiometer.

Now the rapid change in hydrogen-ion concentration which occurs at the " end-point " of a titration may be detected by this method as a

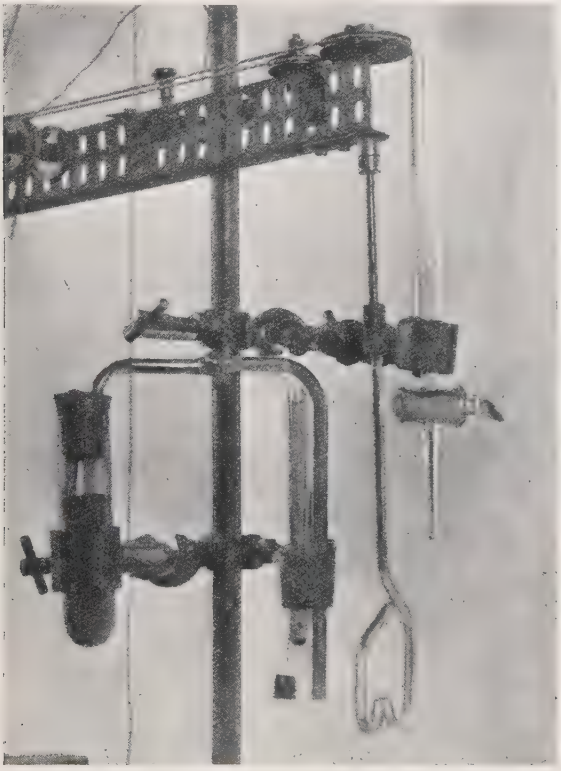

FIG. 1.—The electrodes, etc., the mechanical stirrer and the burette. The titration beaker, into which the stirrer and the exposed electrode dip, is placed in position and supported by a wooden block.

rapid change in potential. And that point in the titration where this change in potential is most rapid, is the end-point. This, the Potentiometric method of titration, has been discussed in detail by Kolthoff and Furman (**2**), and a number of practical applications of it are excellently summarised by Callan and Horrobin (**3**).

The most usual method is to measure the E.M.F. by potentiometer and galvanometer, at intervals as the titration proceeds, and to express increment of E.M.F. as millivolts per c.c. of alkali added. This factor,

termed " dE/dx " by Callan and Horrobin, is greatest at the end-point. The increments of alkali are, of course, made progressively smaller as the end-point is approached. Table I represents the titration of 25 c.c. of N/10 HCl with N/10 NaOH.

The end-point is read from the table as 25·05 c.c.

Greater accuracy may be attained if the increments of alkali near the end-point are made still smaller. Indeed, the accuracy with which the burette can be read is probably the limiting factor. The end-point may therefore be read direct from the figures ; the plotting of a curve is superfluous.

The performance of a titration in this manner is a lengthy operation, but in practice it is not necessary to take more than five accurate readings of the potentiometer, as is shown later. Moreover, in the apparatus described below, the galvanometer is replaced by a pair of head telephones, with an interrupter in the circuit, a modification which causes a great saving in time. Actually, a complete titration occupies only three or four minutes.

III. Description of the Apparatus.

The electrodes and their vessels (Fig. 1) are very simple. The standard half-cell used is not a calomel half-cell, but the standard quinhydrone half-cell of Veibel (**4**). It is a medium-sized tube, containing a buffer solution (pH 2·2) saturated with quinhydrone. The exact value of the buffer solution need not be known, as absolute measurements are not to be made ; a solution of pH 2·2 is found to give convenient readings on the potentiometer. The tube is stoppered with a rubber bung pierced by two holes. The electrode is a square centimetre of gold foil attached to a platinum wire which is fused into the bottom of a small glass tube. This tube passes through one of the holes in the bung, and contains mercury, with which contact with the external lead is made.

The twice-bent glass tube which contains the KCl-agar bridge passes through the other hole in the bung. A small bulb is blown in this tube to frustrate the tendency of the jelly to slip bodily out of the tube. The bridge is prepared as follows : 50 c.c. of distilled water is heated on the water-bath to near boiling-point, and 1·5 gm. of agar-agar is then added. Care should be taken to avoid air bubbles. After about five minutes, 20 gm. of pure KCl is added, and after a further five minutes, one end of the glass tube, which is previously heated in hot water, is inserted into the mixture, and enough sucked up to fill the tube, which is then cooled under the tap. It is well to slip a short length of rubber tubing over each end of the glass. Not only does this make filling easier, but when the rubber is removed after the jelly has set, the tube is left quite full ; if no rubber is used the jelly, contracting as it cools, withdraws a little up

the tube, so that proper cleaning between titrations is difficult. The jelly loses KCl when in use, and has to be replaced at intervals. It may last from three to fifteen days, but this does not seem to depend on the extent to which it has been used.

Titration is carried out in an ordinary beaker. The electrode in this is exactly like that in the other half-cell. Another rubber bung is slipped over the tube which holds the bridge, and the tube into which the platinum wire is fused is held in a second hole in this bung. As Figure 1 shows, the entire assembly is supported by an ordinary retort clamp.

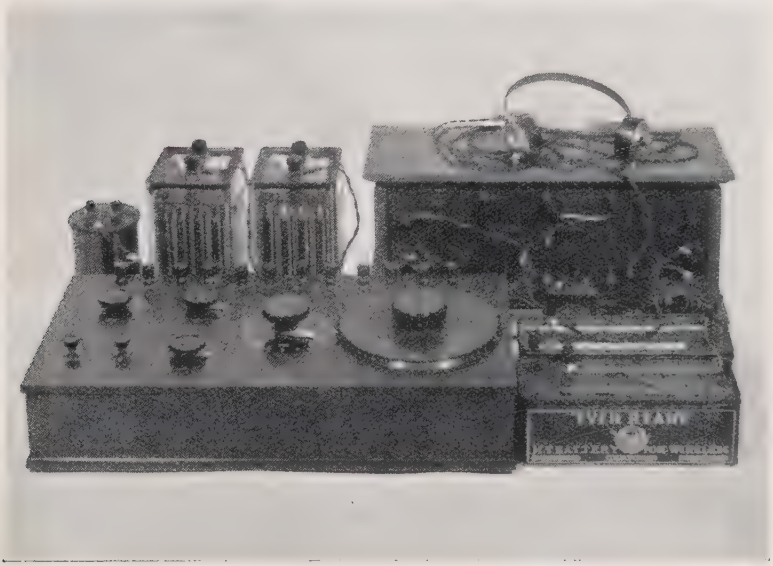

Fig. 2.—The potentiometer and amplifier, and their batteries. The interrupter is kept at the other end of the bench.

A flashlamp bulb in a small metal reflector, and a hand lens, are supported in a wire frame which slides up and down the burette, that it may be more accurately read.

Hand stirring was practised at first, but this proved inadequate, as additions of alkali were not distributed evenly for some time. A mechanical stirrer was therefore arranged, driven by a small electric motor. The power is transmitted by a belt working over a system of pulleys. Meccano components were used for this, as may be seen in Figure 1.

Figure 3 shows that the electrodes are directly connected to a reversing switch, the use of which is illustrated in Table I. Then they pass to the potentiometer and the interrupter respectively. The potentiometer (Fig. 2) used is the "Slide Wire Potentiometer (Modified Form)" of the

Cambridge Instrument Co., Ltd., which is a precision instrument, and was obtained with a view to making hydrogen-ion concentration measurements. But for titrations only, a much cheaper instrument would suffice, since absolute measurements of E.M.F. are not required. Good results could probably be obtained from an improvised potentiometer.

A two-valve amplifier is placed before the head telephones, as was done by Poole (**5**). This was constructed from the standard components sold for radio sets, and contains two transformers, one of which comes before the first valve. As an output transformer is placed between the

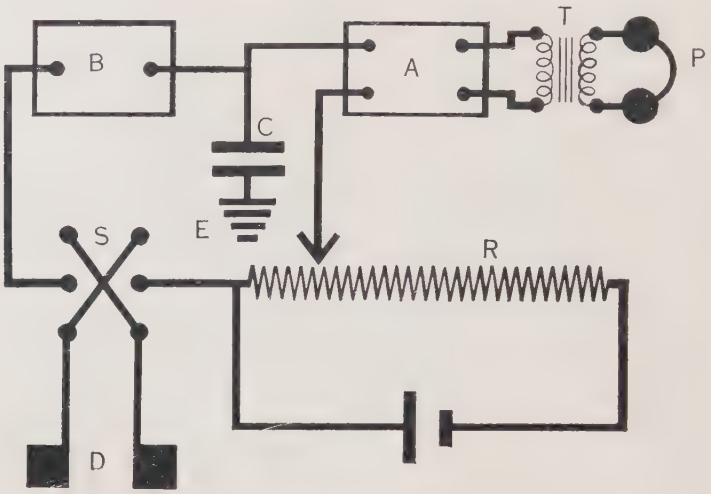

Fig. 3.—The circuit used. The internal circuits of the interrupter and of the amplifier are omitted, and the potentiometer circuit is reduced to its simplest form.

A, amplifier; B, interrupter; C, 2-microfarad condenser; D, electrodes; E, "earth"; P, telephones; R, potentiometer; S, reversing switch; T, output transformer.

second valve and the telephones (although not actually incorporated in the amplifier), the batteries of the amplifier are completely insulated from the remainder of the apparatus. The amplifier is built into a wooden case which is lined with copper sheet, to minimise "interference" from the motor which drives the interrupter. This copper sheet, and the negative terminals of the amplifier batteries, are connected to "earth." "Interference" is further reduced by a two-microfarad condenser between "earth" and the primary of the first transformer.

Several interrupters have been tried. A Meccano assembly, which seemed to be superior to the buzzer device of Poole (**5**) and to the Meccano assembly of Poole and Atkins (**6**) (both of which were tried), was used for some months. Two teeth out of every three were removed from a

heavy-toothed wheel, and the gaps were filled with sealing-wax. This composite wheel was rotated by an electric motor between two pieces of clock spring, pressed firmly against it by rubber buffers. Contact between the springs was made and broken ten times in each revolution. This was very satisfactory, except for the rapidity with which the sealing-wax wore away. When the apparatus had established itself as permanent, a new interrupter was designed, and was manufactured specially by the General Electric Company, Ltd. A motor, driven at 1800 r.p.m. by a 12-volt accumulator, bears on an extension of the armature shaft an extra commutator, carefully insulated from the

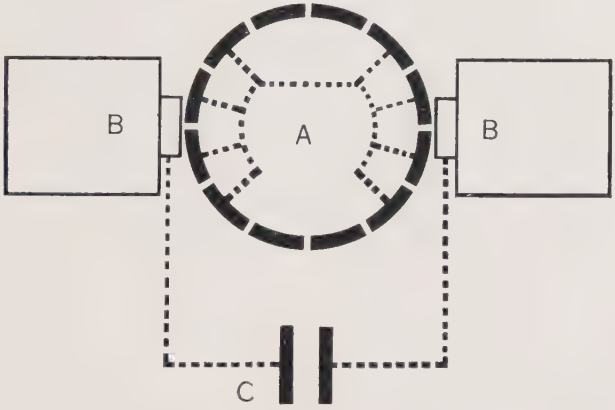

Fig. 4.—Diagrammatic view of the interrupter, showing the electrical connections as broken lines.

A, end view of extra commutator on the armature shaft of the motor; B, sprung carbon brushes, between which contact is made and broken; C, 0·5 microfarad condenser.

armature. Figure 4 shows how contact is made and broken between the two carbon brushes. A 0·05 microfarad condenser is connected across the brushes, and almost abolishes "interference." There is very little mechanical noise.

IV. Procedure in Titration.

The acid solution is placed in the beaker. When the solution to be titrated is alkaline, it must first be made acid by addition of a known amount of acid. If this is not practicable, e.g. when a precipitate would form in acid solution, the titration cannot be performed.

Quinhydrone is added to the solution in the beaker. Its small solubility causes a small quantity to saturate the solution, and this is usually done. But the result does not seem to be affected if the quinhydrone does not saturate.

The acid solution is usually diluted to a "standard volume," suited

to the type of titration. Thus, at Millport, it was necessary to make numerous titrations in which the acid solution was 25 c.c. of 0·1N HCl, partially neutralised by alkali distilled into it, and already diluted to about 190 c.c. The "standard volume" was therefore fixed as 200 c.c., and all the acid solutions in this series of titrations were diluted to this volume. If the titration does not belong to such a series, this dilution is not made. The "standard volume" for any series is made as small as possible, for if a relatively large volume of water be added, the CO_2 dissolved in it may appreciably alter the pH value of the whole.

When, in every titration in such a series, the acid solution has the same volume, the same E.M.F. marks the end-points, provided, of course, that the pH of the buffer solution in the standard half-cell remains constant. Actually this does not remain quite constant, because this solution takes up KCl from the KCl-agar bridge, and is, on this account, periodically renewed. Also, the amount of alkali added, during titrations, naturally varies slightly, so that the volumes at the end-points are not quite the same throughout a series. It is not, therefore, possible to use the Pinkhof method, in which the potentiometer would be set to the known end-point value, and alkali run in until no noise is audible in the telephones. But the E.M.F. at the end-point may be predicted within a few millivolts, so that the E.M.F. at any stage is an excellent indication of the extent to which the titration has proceeded.

In practice, therefore, accurate readings are not taken until within about 1 c.c. of the end point. The interrupter-telephone combination, being completely "damped," allows a rough reading to be taken in a few seconds, and the four or five accurate readings which are necessary, may be taken in two or three minutes. Between each addition of alkali from the burette the liquid in the beaker is very thoroughly stirred, and then the E.M.F. is read. The results are tabulated as in Table I, and the end-point is read direct from this.

The electrodes are subject to polarisation, so that the potentiometer switch should not be held down continuously while a reading is being taken.

If the end-point is overshot, the titration may usually be "brought back" by addition of acid, without serious error.

As there is no galvanometer, and as all the apparatus has sufficient mechanical strength, the whole assembly may be taken to sea, and there worked. It was for this reason that the interrupter was designed to run from an accumulator.

The apparatus is quite independent of colour and turbidity in the liquid. It has been in regular use at Millport for several months, and has been found quite reliable. The accuracy obtainable varies with the strength of the solutions titrated. Successive titrations of 0·01 HCl

against 0·01 NaOH tally within 0·02 c.c. This, of course, does not necessarily imply that the absolute accuracy is as high as this, but relative results have been adequate for the purposes for which the apparatus has been intensively employed.

V. pH Measurements.

The apparatus is perfectly suited to the measurement of hydrogen-ion concentrations. Smaller electrode vessels are then used, and the standard half-cell is either a calomel half-cell or a quinhydrone half-cell containing a buffer solution of accurately known pH. A single E.M.F. is determined, and then a simple calculation should then give the pH of the liquid under test, as is described by Biilmann (**1**) and Clark (**7**). Unfortunately this has been a complete failure, the results being extremely erratic, owing, doubtless, to some fault in detail, at present undiscovered.

I have to thank Mr. H. B. Moore for considerable help in the designing and in the construction of the stirring apparatus and the various interrupters which have been tried.

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A Contribution Towards the Life-History of the Spur-Dog.

By

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With 16 Figures in the Text.

The object in publishing these notes on the Spur-Dog, *Acanthias vulgaris* Risso, is to show the close resemblance, in the distribution of the sizes and sexes, between this fish and the Hake. The Hake will be dealt with in a future paper.

The work has been done during voyages in which the Hake has been the principal object of research. The data on Dogfish have therefore been collected at odd times during a very busy programme on the Hake, and this must be my apology for inadequacy or discontinuity in the figures presented. I would especially thank my colleague, Mr. W. Johnston, and my friend, Mr. C. E. D. Enoch, for their willing help in this entirely unofficial work; and Mr. J. Armitage Robertson for his help in the arrangement of the text.

I. SIZE, SEX, AND DEPTH.

A good series of measurements were made during the cruises of the Ministry of Agriculture and Fisheries' research vessel, *George Bligh*, to the western hake grounds in August, 1928. The position of the stations may be seen in the chart in Figure 1.

The material was collected by using a full-size Vigneron-Dahl trawl, with the cod-end covered by fine-meshed shrimp-netting. One can therefore be certain that no small specimens can have slipped through the meshes and have thus been lost.

The stations worked fall into three main groups, as follows :—

Banks-Westward Group.	Stations "between the Banks," Cockburn Bank, and on the Westward Ground.
Fastnet Group.	Stations Bantry Bay, Galley Head, and Inner and Outer Fastnet.
Galway-Bull Group.	Stations "below the Bull," Galway Bay, i.e. off the Aran Islands, and, finally, inside the Aran Islands.

Station 18, about midway between the Banks-Westward and the Fastnet groups of stations, is considered separately.

Where a depth is referred to, the mean depth of the hauls which supplied the data is meant. The data will be found in the Appendix, Table XIII, where the actual frequency at each 5-cm. group is denoted by an upright, the percentage frequency by an italic numeral.

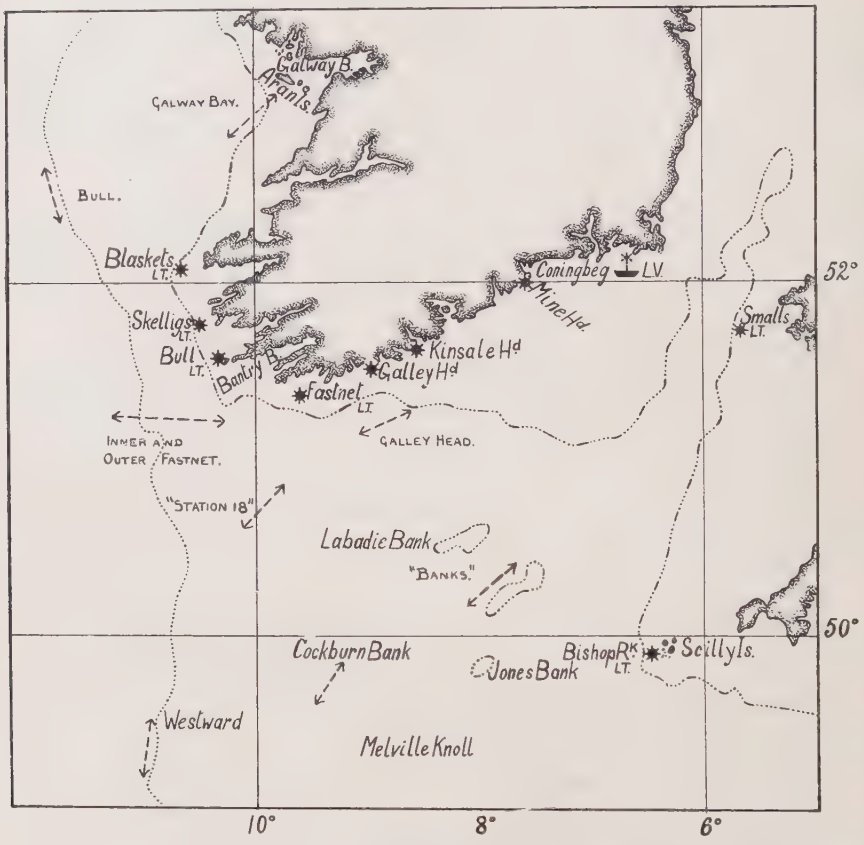

Fig. 1.—Map of South-Western Area, showing the approximate position of the stations sampled, except Bantry Bay, and Inside Aran Islands (Galway Bay).

The Fastnet Stations.

In Figure 2 four pairs of curves are drawn. The pecked line refers to males, the continuous line to females. The curves show the percentage of the fish measured, which were present in each 5-cm. group, each sex being separately considered. The grouping was as follows : more than 25 but less than 30 cm., more than 30 but less than 35 cm., etc. In the figures, the plotted point is at the mid-point of the group.

The uppermost pair of curves refer to the fish measured in Bantry Bay, at a mean depth of 30 fathoms. Both males and females show a well-marked mode at a length, calculated by Wollaston's "three point" method (Wollaston and Hodgson, 1929), of 34·21 and 34·20 cm. respectively. Both curves show a second mode at about 42 cm. (the exact modal length cannot be calculated by Wollaston's method), and a third mode, at 67·5 cm. in the female, and 68·5 cm. in the male. The curves show that the males in the sample tend to be larger than the females, for, in the first mode, 47·8% of the females, but only 39·8% of

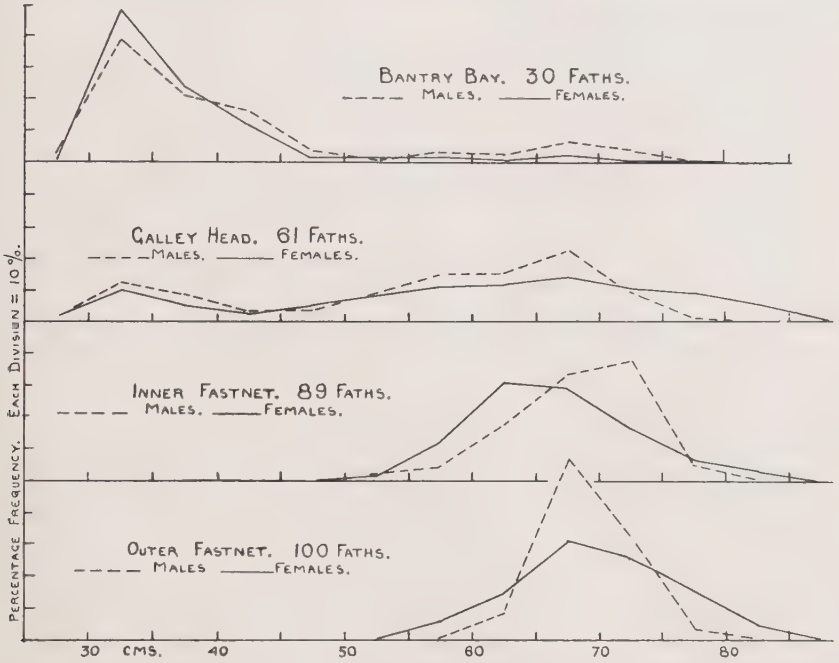

FIG. 2.—The Fastnet Region. Percentage frequencies in the 5-cm. groups of measured fish. *George Bligh*, August, 1928. Data from Table XIII.

the males, in the second mode, at about 42 cm., 12·0% of the females, but 15·2% of the males, and in the third mode, at 67 cm., only 2·2% of the females, but 6·3% of the males, are present. In confirmation of this, the median for the females is found to be 35·4 cm., for the males, 37·3 cm.

The two curves for the Galley Head measurements, at a mean depth of 61 fathoms, show clearly how, with the deeper water, the size of the dogfish has increased. The first mode, at a calculated length of 33·58 cm. in the female, and 34·60 cm. in the male, has a slightly lower modal length than in Bantry Bay, but, on the other hand, only 10·8% of the females and 11·3% of the males are present at this mode. The Bantry

mode at 42 cm. is not indicated, but there are two distinct modes, one at about 58 cm., the other at 66·52 cm. in the female (calculated modal length) and 66·67 cm. in the male. Both these modes are foreshadowed in the Bantry sample, but very few fish are present in them. In the Galley Head sample they predominate, with 14·7% of the females and 23·0% of the males. In this sample also, therefore, there is a tendency for the males to be larger than the females; this may be seen in the higher percentage of males than of females in the modes at 58 and 66 cm.; but in the medians, which are 62·7 cm. for females, and 60·0 cm. for males, the reverse is apparent. This is due, however, to the number of very large females in the sample. As the Appendix, Table XIII, shows, no fewer than 5·8% of the females are between 80 and 84 cm. in length, and 3·5% between 85 and 89 cm. As a later section will show, these are pregnant females which have migrated inshore to give birth to their young.

The two curves for the Inner Fastnet measurements show a further increase in size associated with the increased depth (89 fathoms). Small fish are not present; both males and females give an unimodal curve, with a calculated modal length of 64·81 cm. in the female, and 70·33 cm. in the male. The medians are 65·9 cm. in the female, and 69·2 cm. in the male. In this sample, therefore, the males were distinctly larger than the females.

Finally, the Outer Fastnet measurements (100 fathoms) also give unimodal curves for both males and females. Here, however, the females are larger than the males, for the calculated modal lengths are 69·17 cm. in the female, and 68·93 cm. in the male. The medians are 69·9 in the female, and 68·9 in the male. It is important to notice that, in the deepest water, 100 fathoms, there are 5% of the females at 80 to 84 cm., and 1·4% at 85 to 89 cm., whereas at 89 fathoms there are only 2·9% of the females at 80 to 84 cm., and 0·7% at 85 to 89 cm.

In these four samples from the Fastnet group of stations, therefore, we may see the progressive increase in length of the dogfish with increase in depth, manifesting itself in (*a*) a movement of the modal lengths to the right, (*b*) an increasingly higher proportion of the fish at the higher modes, and (*c*) an increasingly higher median.

The Banks-Westward Stations.

In Figure 3 are drawn three pairs of curves. These refer to the samples collected on the three stations comprising the Banks-Westward group (Figure 1). As the Appendix, Table XIII, shows, the data from these stations are less abundant than those from the Fastnet group of stations, but their interpretation is no less clear and unequivocal. In Figure 3,

as in Figure 2, the pecked line refers to the males, the continuous line to the females.

In the Banks sample (69 fathoms) two modes are seen, with calculated modal lengths of 33·55 cm., and 55·30 cm. in the female, and 33·80 cm. and 52·18 cm. in the male. The second modal length is therefore slightly higher in the female than in the male ; on the other hand, in the first mode 33·8% of the females, but only 18·4% of the males are present, and in the second mode, 11·5% of the females, but 21·9% of the males. Thus, at this station, as at the Bantry Bay, Galley Head, and Inner Fastnet stations, the males present have a greater size than the females. This is

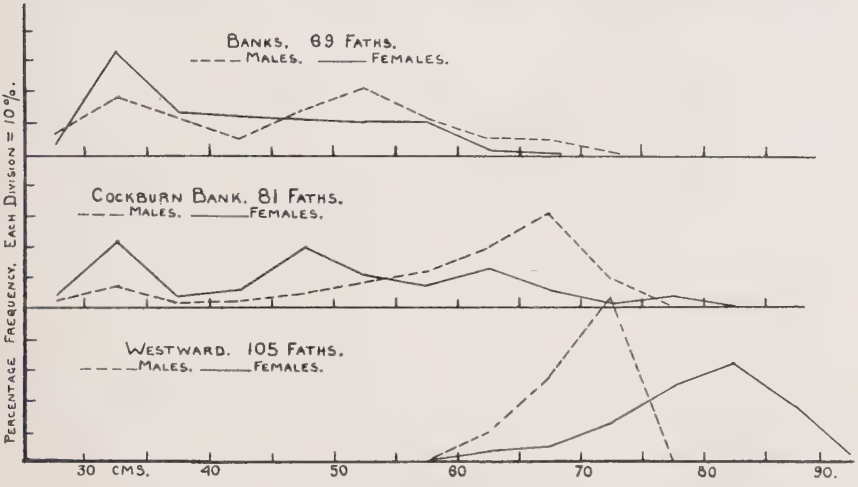

FIG. 3.—The Banks-Westward Region. Percentage frequencies in the 5-cm. groups of measured fish. *George Bligh*, August, 1928. Data from Table XIII.

further shown by the medians, namely, 39·5 cm. in the female, and 47·8 cm. in the male.

The measurements made on the Cockburn Bank (81 fathoms) show that, in this deeper water, the length of the fish of both sexes has increased. Three distinct modes are shown by the curve for females, at calculated modal lengths of 32·37 cm., 48·32 cm., and 63·07 cm. The first of these modes is plainly identical with that shown at 33·55 cm. in the Banks sample, but, at 81 fathoms, only 21·5% of the females are present at this mode, as compared with 33·8% at 69 fathoms, while at the second and third modes, at 81 fathoms, 19·5% and 12·7% of the females are present. The males show two distinct modes, which give calculated modal lengths of 32·31 cm. and 66·37 cm. The first of these is identical with the first of the modes in the curve for the females, but only 7·3% of the males are present at this mode, as compared with 21·5% of the females. The second mode in the curve for males, at 66·37 cm., contains

no fewer than 30·6% of the males. Here again, therefore, the males in the sample are distinctly longer than the females in the sample, and the medians show this well, that for the males being 63·1 cm., for the females, 48·9 cm.

Finally, the Westward sample shows curves of the same type as the Outer Fastnet sample in Figure 2. The females are distinctly larger than the males, the curves for both sexes are unimodal, with calculated modal lengths of 81·79 cm. in the females, and 71·40 cm. in the males. The medians are 81·0 cm. in the females, and 70·5 cm. in the males.

In the Banks-Westward series of stations there is shown the progressive increase in size of the dogfish of both sexes, with increase of depth, and, except in the Westward sample, the larger size of the males, as compared with the females, in any given sample. When the Banks-Westward stations are compared with the Fastnet stations, however, three points arise which must be noted, as they will be referred to later.

Firstly, there is a different relation to depth in the two groups of stations. The Banks curves, when compared with the Galley Head curves, show, in spite of the closely similar depth, a smaller size of dogfish ; this can be best expressed by comparing the medians, which are 39·5 cm. in the female, and 47·8 cm. in the male, in the Banks sample, at 69 fathoms ; but 62·7 cm. and 60·0 cm. in the males and females respectively, in the Galley Head sample, at 61 fathoms. A comparison of the Inner Fastnet (89 fathoms) with the Cockburn Bank (81 fathoms) shows the same phenomenon.

Secondly, no such shallow water was worked in the Banks-Westward group of stations as was worked in Bantry Bay (30 fathoms), but, on the whole, small newly-born dogfish were much scarcer in the Banks-Westward than in the Fastnet group of stations, and had a smaller size. The modal lengths were 33·5 cm. and 33·8 cm. in females and males in the Banks sample, but 34·2 cm. in male and female in the Bantry sample. The difference, though slight, may be significant.

Thirdly, whereas, in the Fastnet group of stations, the largest females tended to be well represented in the shallow water stations, such as Bantry Bay, and especially Galley Head, in the Banks-Westward stations they are almost absent from the Banks and Cockburn Bank stations. On the other hand, they were concentrated in the deep water on the Westward ground to a much greater degree than on the Fastnet grounds at approximately the same depth. The impression is given that, in the Fastnet region, there had been a migration of the large females into shallow water, which had not yet taken place, or had only just begun, on the Banks-Westward stations at the time of the voyages.

The Galway-Bull Stations.

As the Appendix shows,* dogfish were very scarce on the Bull grounds, probably on account of the comparatively great depths fished there. The few specimens taken were found in the shallowest hauls (98 and 105 fathoms). The distribution of Acanthias with depth has been discussed elsewhere (Hickling, 1928), and it was shown that, in the Faroe-Shetland Channel, and off the West coast of Scotland, this fish was taken at every depth from 90-100 to 500-520 fathoms. The scarcity of dogfish in the deeper water on the Bull and Westward grounds may well be due to a regional, or, much more probably, a seasonal, variation in distribution.

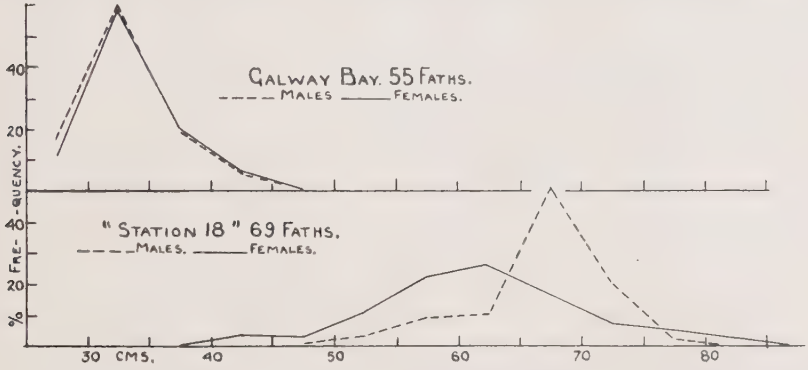

Fig. 4.—Galway Bay and Station 18. Percentage frequencies in the 5-cm. groups of measured fish. *George Bligh*, August, 1928. Data from Table XIII.

The 22 dogfish taken on the Bull grounds were, with five exceptions, between 60 and 90 cm. in length, but the sample is too small to be worth further discussion.

The Galway Bay sample consisted almost wholly of young newly-born fish, as Figure 4 shows. There is a single mode, at a calculated modal length of 32·99 cm. in the females, and 32·75 cm. in the males. The curves for male and females, however, fit more closely than in any other sample. Besides these young fish, there were six large females of 70 to 93 cm.

The third station, at 21 fathoms inside the landlocked waters of Galway Bay, was only sampled with a single haul of one hour's duration. This haul yielded 38 dogfish, which showed a length-distribution as follows : —

Length	25 to 29	30 to 34	35 to 39	40 to 44	45 to 69	70 to 74	75 to 79	80 to 84	85 to 89	90 to 94	95 cm. to 99 cm.
Frequency	1	8	6	7	0	2	2	4	5	2	1

* Table XVIII.

The dogfish found in this very shallow water, therefore, fell into two sharply defined groups, the one, of small fish between 25 and 44 cm., the other, of large fish between 70 and 99 cm. Of the large fish, all but one were females.

A comparison has already been made between the Banks-Westward and the Fastnet groups of stations, and the conclusion was drawn that, among the large females, there was a migration inshore, which had not yet commenced in the Banks-Westward region, but was well advanced in the Fastnet region. It may be suggested that, in the Galway-Bull region, this inward migration of large and, as we shall see in a later section, pregnant females, was even more advanced than in the Fastnet region. For in very shallow water in Galway Bay, the fish consisted almost wholly of pregnant females and newly-born young, while in deeper water, in 55 fathoms, the fish consisted almost wholly of newly-born young, with a few pregnant females. The inshore migration of pregnant females, therefore, which, according to Travis Jenkins (1925), bear their young in very shallow water of 3 to 6 fathoms, is complete in the Galway-Bull region, is far advanced in the Fastnet region, but has hardly commenced in the Banks-Westward region.

The very great abundance of newly-born dogfish in Galway Bay is further evidence of this completion of the birth of the young. They were abundant at 55 fathoms in the Galway-Bull region, whereas, in the Fastnet region, they were most abundant at 30 fathoms, and comparatively scarce at 61 fathoms. This difference is probably the consequence of the earlier birth of the young in the former region, for, according to Travis Jenkins (*loc. cit.*), the young dogfish move away from shallow water shortly after birth.

The sample of dogfish taken at Station 18, midway between the Banks-Westward and the Fastnet regions, furnishes percentage frequency-curves which are shown in the lower part of Figure 4. Both males and females show one predominant mode, at calculated modal lengths of 61·12 cm. in the female, and 68·12 cm. in the male. The medians are 61·4 cm. in the female, and 67·7 cm. in the male. This sample, therefore, furnishes further evidence of the larger size of the males at any given depth, such as has already been shown to be the case in both the Banks-Westward and Fastnet regions.

Both males and females show a mode at a lower length also, indicated by a flattening of the curves at about 45 cm. in the female, and 58 cm. in the male.

When the frequency-curves are compared with the series in Figures 2 and 3, it is clear that the sample from Station 18 more closely resembles the Fastnet samples than the Banks-Westward samples, having regard to the depth at which the sample from Station 18 was fished.

The Sex-Ratio.

Figures 2, 3, and 4 have represented the percentage frequency-curves of each sex considered separately. They therefore give no information as to the relative numbers of the sexes. Table XIII in the Appendix will show that the sex-ratio shows considerable variation in the samples, but is related to depth in such a way, that, down to a certain depth, the percentage of males increases, but, beyond that depth, decreases, until, in the deepest water, females form the great majority of the fish. The sex-ratios must be interpreted in the light of the length-distributions.

In the Banks-Westward region, the percentage of females was as follows :—

Banks Station	69 fathoms	54·9% females.
Cockburn Bank Station	81 fathoms	37·8% females.
Westward Station	105 fathoms	84·8% females.

In the Fastnet region, the percentage of females was as follows :

Bantry Bay Station	30 fathoms	59·2% females.
Galley Head Station	61 fathoms	61·3% females.
Inner Fastnet Station	89 fathoms	69·9% females.
Outer Fastnet Station	100 fathoms	88·0% females.

At Station 18 there were 52·2% females, and in Galway Bay 56·9% females.

It will be clear, from what has been said in the foregoing pages, that, in both males and females, there is a segregation according to size, such that the larger fish tend to be found in deeper water. Since in any given sample from shallower water the males tend to be larger than the females, the males are distributed in shallower water than the females.

Ford (1921), whose work will be constantly referred to in this paper, found that male and female dogfish are born in approximately equal numbers, and at the same length. The segregation of males in shallower water than the females will therefore tend to result in a sex-ratio, except in very shallow water, of more than 50% females. For example, in the Galway Bay sample, from a depth of 55 fathoms, the dogfish, which were, by their length, plainly newly-born, already showed 56·9% of females, and in Bantry Bay, where conditions were much the same, 59·2% females. This difference in the distribution of the sexes is the first factor affecting the sex-ratio.

But the females grow to a much greater length than the males. Ford's data show that the largest male examined during his work was 83 cm., but his largest female was 110 cm. in length. My own figures, as in Table XIII, show the same fact equally clearly. Therefore, since females

grow to a greater length than the males, and since the dogfish, other things being equal, are segregated according to size, with increase of depth, in the deepest water we should expect to find only big fish, and therefore chiefly female fish. This may be seen in the Westward and Outer Fastnet samples, where the percentage of females is respectively 84·1 and 88·0. This is the second factor affecting the sex-ratio, but it also acts in a somewhat unexpected way, as the next section will show.

The smaller size of the males is very well known as a general phenomenon among fishes. In the case of the Plaice (Wallace, 1907), the Cod (Saemundsson, 1923), and the Hake (Birtwistle and Lewis, 1924 ; Belloc, 1922) at least, it is due to a failure on the part of the males to maintain the rapid rate of growth shown by the females. The older year-groups among the males of these fish are therefore compressed into a much narrower range of length than the females, and, although Wallace rightly suggests that male Plaice are more viable than the females, there will clearly tend to be a region in the scale of length where few year-groups of females, but many year-groups of males are present. At these lengths the males will tend to be more abundant than the females. In the case of the Dogfish, we have seen that the fish are distributed by size according to depth. Therefore there will be a certain depth at which males will predominate over the females. This predominance may be seen in the Cockburn Bank sample, in which there are only 37·8% of females.

This should be regarded as the normal distribution of the sexes, with depth, in the Spurdog. In the shallowest water there should be a slight predominance of males, then a region where there is a slight predominance of females, then a somewhat restricted region where males greatly predominate, and finally, at still greater depths, a gradually increasing predominance of females. It is, therefore, hardly possible to speak of the sex-ratio among dogfish as though this were a constant ; it will clearly vary with depth, and also, almost certainly, with season.

But it has also been shown that there is a shoreward migration of pregnant females. The presence of these females, in any numbers, must tend to reverse the sex-ratio in those regions where males would, on hypothetical grounds, predominate. In the Galley Head sample, and, to a lesser extent, in the Inner Fastnet sample, these pregnant females were present in some abundance, hence none of the stations in the Fastnet series shows such a predominance of males as the Cockburn Bank Station, where the inward migration of the pregnant females had not commenced.

This alteration of the hypothetical sex-ratio in dogfish by the inward migration of the pregnant females reaches its extreme, of course, in the very shallow station inside Galway Bay, at 21 fathoms, in which, of the larger group of fish, 93·8% were females.

For comparison with these results, data collected during the exploratory voyages of the *Florence Brierley* of Fleetwood, in March and April, 1927, are of value, and afford good confirmation. Three cautionary remarks must be made. Firstly, the material is usually much scantier than that available from the stations of the *George Bligh*; secondly, an ordinary commercial cod-end was used, without a covering of shrimp-mesh; and thirdly, the shallowest water worked was 96 fathoms.

In Figure 5 are plotted the points representing the variation in sex-ratio, with increase of depth, as shown by the *Florence Brierley* samples. The abscissa represents the depth in fathoms, the ordinate, the percentage of females. The data will be found in the Appendix,

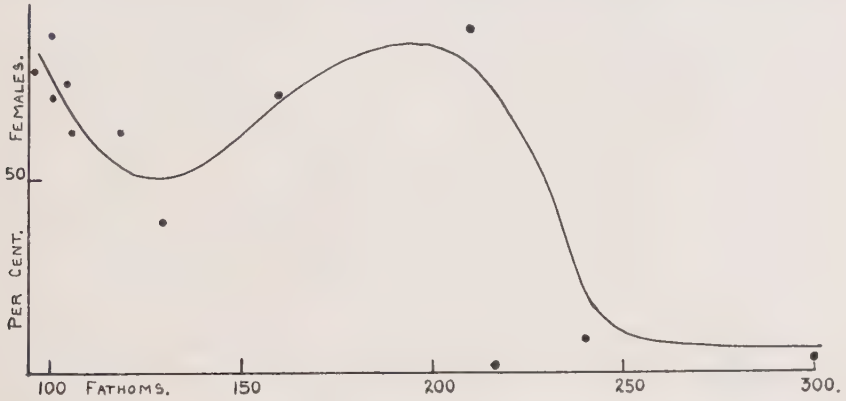

FIG. 5.—Variation in sex-ratio with depth. *Florence Brierley*, April, 1927. Data in Table XIV.

Table XIV. A line is drawn through the plotted points, to show the general trend.

It is evident that, from the shallowest water worked down to about 130 fathoms, the percentage of females decreases. It then increases from 130 to about 200 fathoms. This fluctuation is perfectly understandable from what has been said earlier in this section. There is a region where, for the reasons there stated, the males must tend to predominate, and, in these samples, 130 fathoms is, roughly, the centre of this region. Beyond this depth, females become dominant, until 90% of females is found at 210 fathoms. Moreover, the pregnant females were most abundant in the deep water; at this time, therefore, there was no inshore migration of pregnant females to mask the concentration of the males at the intermediate depth.

Something quite new shown by Figure 5 is the presence, in very deep water, of shoals of dogfish consisting exclusively of mature males. It may be taken as certain that these males were living pelagically, and were caught during the hauling or shooting of the trawl.

Sexual Maturity, Pregnancy, and the Embryo.

Ford (*loc. cit.*) finds that, in the male dogfish, sexual maturity sets in at about 59–60 cm., but, in the female, not until between 70 and 80 cm. The smallest pregnant female in his samples was 72·8 cm. in length, but he concludes that a female "before becoming mature, undergoes an extended adolescent period in which her first set of eggs are developing in the ovaries. The specimens under 70 cm. in length were quite immature, and no conspicuous eggs were present in the ovaries."

In Figure 6 are drawn two curves, showing the percentage, respectively, of mature and immature males at lengths between 52 and 66 cm. The earliest mature fish was 55 cm. in length, the latest immature fish 63 cm.

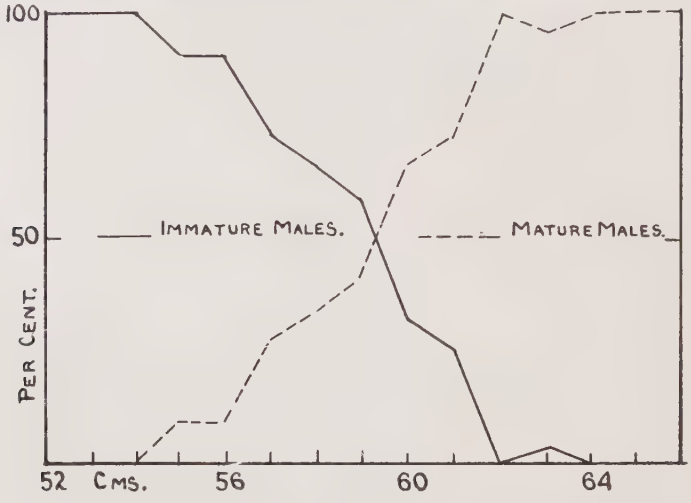

Fig. 6.—Onset of maturity in male dogfish. All stations combined, *George Bligh*, August, 1929. Data in Table XV.

The curves cross at some point between 59 and 60 cm., so that I can entirely confirm Ford. The data are given in the Appendix, Table XV.

The smallest pregnant female found in my samples was 64 cm. in length, but I can confirm Ford's conclusion that pregnancy generally sets in between 75 and 80 cm. In Figure 7 the percentage of pregnant females in the total females, at each 5-cm. group, is shown graphically. The data are to be found in the Appendix, Table XVI. The curve shows its most rapid rise from 75–79 to 80–84 cm., but it never reaches 100% owing to the presence of newly-spent females.

In Table I the pregnant females found at each station are represented by a black dot. It should be said in passing, that these data on pregnancy are based on the females dissected for the weighing experiments to be described in the latter half of this paper.

TABLE I.

Length Group.	Banks 69	Cockburn Bank 81	Westward 105	Bantry Bay 30	Galley Head 61	Inner Fastnet 89	Outer Fastnet 100	Bull 130	Galway Bay 55	Inside Islands 21	Station 18 69
55–59											
60–64		·									
65–69			·								·
70–74		·	··	·		·	·				
75–79		·	·		·				···		·
80–84			····	·····	·····			··	·····	···	
85–89	··		····	···	··		··		·····	··	·
90–94			·	··					···	··	
95–99										·	

The table shows the occurrence of pregnancy in the various samples quite sufficiently clearly, without the necessity of weighting for the size of the samples.

Pregnant females were few in the Banks and Cockburn Bank samples,

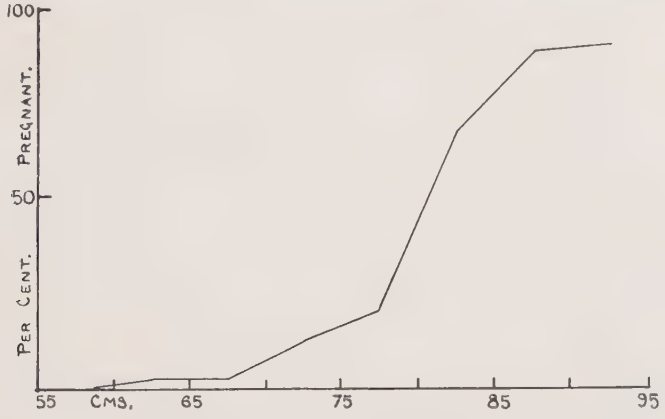

FIG. 7.—Onset of pregnancy in female dogfish. All stations, *George Bligh*, August, 1928. Data in Table XVI.

but plentiful in the Westward sample. In the Fastnet group of stations, pregnant females were plentiful in the Bantry Bay and Galley Head samples, but scarce in the Inner and Outer Fastnet stations, and from the sample from Station 18. In the Galway-Bull region, pregnant females were scarce in the Bull sample, but plentiful in the Galway Bay sample, and in the shallow water inside the Aran Islands.

Recalling what has already been said about the distribution of large females among the stations, it is clear that the distribution of pregnant females is identical with this, and that the inward migration of large females, deduced by an inspection of the frequency-curves, is, in reality, a shoreward migration of pregnant females to bear their young in shallow water. This shoreward migration was far advanced in the Galway-Bull

region, was taking place in the Fastnet region, but had not yet commenced in the Banks-Westward region.

This may be illustrated further by showing the percentage of pregnant females among the potentially pregnant females in the different samples. For this purpose, all females greater than 75 cm. are regarded as potentially pregnant. The data are given in Table II in the text below. In many of the samples, the data are thin, in others, fairly adequate, but in all regions one may see that the pregnant females predominate in the shallow water, and that, in the deeper water, in those regions where the inward migration is farthest advanced (the Inner and Outer Fastnet grounds for example), those mature females remaining are non-pregnant. These are probably newly-spent fish, which have returned to deep water after bearing their young.

Table II.

Percentage of Pregnant Females in the "George Bligh" Samples.

Station.	Depth.	No. of Females greater than 75 cm.	No. pregnant.	% pregnant.
Banks	69	2	2	100
Cockburn Bank	81	3	3	100
Westward	105	15	13	87
Bantry Bay	30	20	13	65
Galley Head	61	19	10	53
Inner Fastnet	89	7	1	14
Outer Fastnet	100	19	3	16
Bull	130	8	2	25
Galway Bay	55	33	32	97
Inside Aran Islands	21	9	8	88
Station 18	69	7	3	43

The results of the voyages of the *George Bligh*, therefore, show us the distribution of pregnant females at the time of the birth of the young, which, as Ford finds, takes place from September onwards. The voyages of the *Florence Brierley*, on the other hand, show that, in the early spring, the pregnant females are found in the deeper water. As the Appendix, Table XIV, shows, the four well-sampled hauls of March 29th and 30th, and March 31st and April 2nd, give clear indication of the shoaling of the pregnant females in deeper water. This, however, is simply the consequence of the segregation of the larger sizes of dogfish in the deeper water, already demonstrated earlier in this paper. The segregation is upset only by the inward migration of the pregnant females in the summer and early autumn.

Ford has measured large numbers of embryo dogfish throughout the seasons, with very instructive results. In my judgment, he proves beyond doubt that the breeding season has definable limits, and that embryonic development is lengthy, taking about 25 months. Ford concludes that "from September onwards, specimens from 23 to 31 cm., inclusive, satisfy the conditions for birth." These results are based on samples of dogfish landed at Plymouth. Owing to this protracted gestation period, "on any one day, the embryos are separable into two or three distinct size groups, according to the time of the year."

I have measured a certain number of the embryos found in the pregnant females fished by the *George Bligh*, and my results entirely confirm Ford's. The embryos fell into two distinct groups. One consisted of embryos between 4 and 7 cm. in length, of which very few were measured, while the larger group consisted of embryos between 18 and 27 cm., of which 233 were measured. In Table III are shown the length-frequencies of the embryos measured in the three regions.

TABLE III

MEASUREMENTS OF EMBRYO DOGFISH, GROUPED BY REGIONS.

Length in cm.	Banks-Westward.	Fastnet.	Galway-Bull.
18	–	1	–
19	–	5	1
20	–	9	4
21	2	9	15
22	8	19	17
23	9	27	10
24	13	10	24
25	5	4	12
26	–	–	5
27	–	–	2
Totals	37	84	90
Mean length	23·3	22·2	23·1

Few measurements are available from the Banks-Westward region, but the Galway-Bull embryos were plainly slightly more advanced than the Fastnet embryos, a fact which is wholly consistent with the suggestion that there is an earlier inward migration of the pregnant females in the Galway-Bull region. But the differences are slight, and it is evident that there would be no great lag in the time of birth of the young as between these three regions.

The length distribution of the embryos in my samples agrees with Ford's August measurements.

In Figure 8 are drawn two curves. The pecked line shows the frequency at each centimetre length of the embryos of the larger group (all stations combined), the continuous line, the length-frequencies of the fish in the first mode of free-living young. The data are given in the Appendix, Table XVII. There is an overlap between the curves. Four fish, between 23 and 25 cm. in length, which have been measured with the free-living young, can probably be neglected, for they were almost certainly squeezed from the parent by the violence of capture. Apart from these, the curve

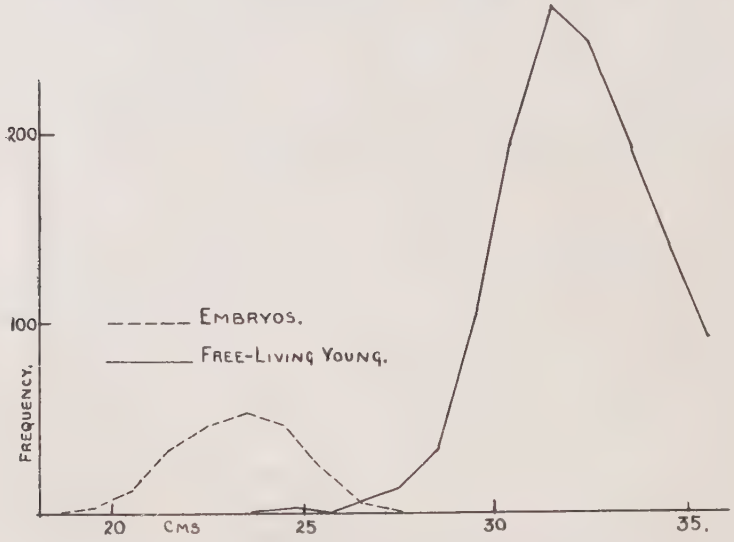

FIG. 8.—Frequency curves of embryos and free-living young of first mode. All stations, *George Bligh*, August, 1928. Data in Table XVII.

for unborn young ends, and that for free-living young commences, at 27 cm.

It is curious that the modes of the curves for unborn and free-living young should be so widely separated. The modal lengths are roughly 23 and 32 cm.—9 cm. apart. There are four possibilities.

(1) Growth may be very rapid immediately after birth.

(2) There may be a periodicity in the growth and birth of the embryos, such that the smallest free-living young belong to an earlier " wave."

(3) There may be a high mortality among the smaller newly-born fish. The resulting survival of the larger fish would effectively shift the modal-length of the free-living young to the right.

(4) The birth of the young may not have yet begun, contrary to what

has been suggested earlier in this paper. The free-living young may therefore belong to last year's brood, which has grown 9 cm. in the interval.

Taking the last suggestion first, it is very unlikely that this is the correct explanation, because Ford finds that unborn embryos may reach a length of 31 cm. ; secondly, because there is a continuity between the curves for unborn and free-living young, in Figure 8, and 9 cm. seems, on the face of it, to be too small an increment in a year ; and, finally, because, in many of the free-living young, the umbilical scar was still plainly visible, pointing to very recent birth.

While the third possibility given above is quite strong enough to be borne in mind, Ford's extensive measurements do not confirm the fourth suggestion, that there is a periodicity in the birth of the young.

When " condition " is dealt with later in this paper, it will be shown that there is a heavy loss in the condition of the liver as between unborn and free-living dogfish ; in my view, growth immediately after birth is very rapid, and is carried out at the expense of the reserve materials stored in the liver of the embryo.

Summing up the results of the first section of this paper, the distribution of the dogfish at the time of the voyages is as follows : the males are present in shallower water than the females, and, owing to the strict segregation of the fish of both sexes according to size, and the smaller size attained by the males, in the deeper water females predominate. These big females are mostly pregnant, and make a migration from the deep to the shallow water to bear their young. The young are born at about 26 cm., and, growing rapidly, move off to deeper water, the males already separating in shallower water than the females. Apart from the inward migration of the pregnant females, the dogfish seem strictly segregated according to size, in such a way that the larger fish are found in deeper water. The same segregation, according to size, was observed during the voyages of the *Florence Brierley*, in the early spring ; it probably holds good at all times of the year.

The inward migration of the pregnant females, and the bearing of the young, seem to proceed from west to east, the process being most advanced to the West of Ireland, and least advanced in the latitude of Cornwall. This roughly-sketched picture will be compared, in the discussion, with Ford's notes on the dogfish landed at Plymouth market.

II. CONDITION.

A considerable number of weighing experiments were made on the Dogfish during the cruises of the *George Bligh*. The degree of accuracy, to be expected in weighings made at sea, is discussed in Section A of my

Hake report (1930). Only larger dogfish, of more than 50 cm., were dealt with in these weighing experiments.

The procedure was as follows : the fish was first measured, then the gut and gonads were removed, and the gutted fish weighed. The liver was then weighed, the stomach-contents, if any, noted, and, if the fish were a female, whether it were pregnant or not. Any embryos were removed and measured.

The data obtained were, length, sex, sexual condition, weight of liver, and weight of flesh. By " flesh " is here meant the gutted fish.

The data are set out in the Appendix, Table XVIII. The dogfish have

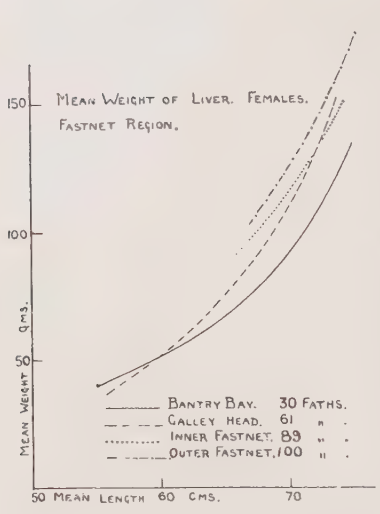

FIG. 9.

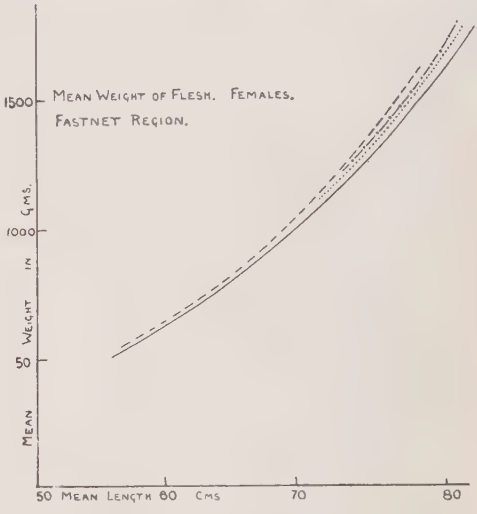

FIG. 10.

FIGS. 9 and 10.—Fastnet Region. Curves showing increase in mean weight of liver (Fig. 9), and flesh (Fig. 10), with increase of length, in immature and non-pregnant females. August, 1928. Data from Table XVIII.

been grouped into three classes, namely, males (without distinction into mature and immature), immature and non-pregnant females, and pregnant females. Each class is further sub-divided into 10-cm. groups, and for each 10-cm. group the mean length, mean weight of liver, and mean weight of flesh has been calculated. Further, the value of the " coefficient of condition " k has been calculated for each 10-cm. category. This " coefficient k " is given by the weight of the liver, or flesh, as the case may be, divided by the cube of the length of the fish. The value so obtained has been multiplied by 100 in order to eliminate two decimal places.

Selig Hecht (1913) published a note on the relation of weight to length in the dogfish *Mustelus canis*. He found that there was no sexual difference in the relation of weight to length in this fish. When weight was

plotted against length, a curve drawn through the plotted points was found to have the form,

$$y = ax^3,$$

where y is the weight, x the length, and a a constant "whose value depends on the units used." He found that the variations in the value of a with length are very slight, and therefore that "the relation of form to mass is clearly indicated by the young fish, and is continued with apparent mathematical accuracy as the fish increases in length and weight." Using his weight determinations, one can show that the value of the coefficient k is highest in the 40–50-cm. group, and decreases until the 70–80-cm. group, after which there is a recovery in the 80–90-cm. group. But it is hardly feasible to compare Hecht's figures with mine, since he has not distinguished, in his means, between females and males, nor between pregnant and non-pregnant females.

An inspection of the data in the Appendix, Table XVIII, will show clearly that the coefficient k is not a constant in the case of either the liver or the flesh, in my observation. In the liver it increases slowly with increase of length, a fact which will be given special emphasis in the discussion, and, in the flesh, as in Hecht's material, it decreases slowly with increase of length. But, for the present purpose, it may be considered constant over a short range of length, and therefore in comparing fish whose mean length varies only slightly from sample to sample. At the same time, this variation renders it risky to compare the mean value of k in samples with a wide range of length. In this section, therefore, the data are divided into length-groups, and the means for the groups compared in the different samples.

First, however, the mean values for all the fish of each biological sub-group, at each station, may be examined. In Table IV below are set out the mean value of k (liver) and k (flesh) in the males, with the mean depth of the stations, and the number and mean length of the fish examined.

Table IV.

All Stations. Males. Mean Value of k (Liver) and k (Flesh).

Station.	Mean Depth.	Number of fish.	Mean length.	Mean value k (liver).	Mean value k (flesh).
Bantry Bay	30	40	67·0	·0229	·280
Galley Head	61	36	65·3	·0267	·290
"Station 18"	69	25	67·8	·0310	·293
Between Banks	69	25	61·1	·0238	·259
Cockburn Bank	81	20	64·5	·0288	·295
Inner Fastnet	89	25	69·9	·0327	·294
Outer Fastnet	100	30	69·7	·0339	·289
Westward	105	6	71·2	·0349	·292

This table shows clearly that the mean value of k (liver) increases with increase of depth. The only discrepancies are the Banks and Cockburn Bank samples, which give lower values than the other stations of comparable depth. But the table shows that these fish also had a lower mean length than those of these other stations. The mean values for the flesh do not show such a definite relation with depth.

In Table V, a similar comparison is made for immature and non-pregnant females.

TABLE V.

ALL STATIONS. IMMATURE AND NON-PREGNANT FEMALES. MEAN VALUE OF k (LIVER) AND k (FLESH).

Station.	Mean Depth.	Number of fish.	Mean length.	Mean value k (liver).	Mean value k (flesh).
Bantry Bay	30	44	64·2	·0263	·289
Galley Head	61	51	66·8	·0298	·306
"Station 18"	69	28	67·4	·0325	·305
Between Banks	69	20	57·9	·0245	·274
Cockburn Bank	81	19	63·3	·0252	·295
Innet Fastnet	89	32	70·3	·0352	·303
Outer Fastnet	100	26	73·5	·0407	·298
Westward	105	8	74·4	·0372	·308
Bull	130	15	75·6	·0409	·314

In immature and non-pregnant females also, there is a very well marked increase in the value of the coefficient k (liver) with increase of depth. As in the males, the stations in the Banks-Westward group give lower values than the other stations of a comparable depth. The mean values for k (flesh) do not show the same relation to depth.

In every case, the mean value for k (flesh) is greater in the female than in the male, and in every case except the Cockburn Bank station the value of k (liver) is greater in the female than in the male.

Finally, in Table VI are compared the mean values for k (liver) and k (flesh) in pregnant females.

TABLE VI.

ALL STATIONS. PREGNANT FEMALES. MEAN VALUE OF k (LIVER) AND k (FLESH).

Station.	Mean Depth.	Number of fish.	Mean length.	Mean value k (liver).	Mean value k (flesh).
Inside Aran Islands	21	8	87·9	·0222	·306
Bantry Bay	30	12	85·3	·0227	·302
Galway Bay	55	33	85·5	·0263	·305
Galley Head	61	9	83·3	·0334	·337
Westward	105	13	82·0	·0351	·322

It is clear, from Table VI, that in pregnant females, as in the other two biological sub-groups of the dogfish, there is a very well marked increase in the value of k (liver), with increase of depth, and that this increase is not shown, at least so distinctly, in the values of k (flesh).

In the Bantry Bay and Westward samples, the mean value for k (liver) is distinctly less in pregnant than in non-pregnant females, that for k (flesh) greater. The latter is at first sight understandable, since the mean length of the pregnant females is much greater than that of the non-pregnant females. Later in this section, it will be shown that, even when the effect of a different mean length is minimised, the liver of the pregnant female is generally lighter, the flesh generally heavier, than in non-pregnant females.

Tables IV, V, and VI show that, in many of the stations, the sampling is fairly adequate, at others, where very few dogfish were found, it is, of course, less satisfactory. But since the values for the coefficient k are not constant with increase of length, it will be necessary to confirm the conclusions drawn from Tables IV, V, and VI, by an examination of the fish divided into 10-cm. categories.

The 10-cm. categories into which the data have been grouped are 50–59 cm., 60–69 cm., etc., the number of weighings from which the mean has been calculated varies considerably from sample to sample, and the reliability of the mean varies accordingly. But, in the Fastnet group of stations, the sampling is satisfactory, and one can regard the results with some confidence. The stations in the Fastnet region will therefore be discussed first, and a comparison will then be made between the Fastnet group of stations and the remaining two groups of stations.

In Figure 9 four curves are drawn. Each curve represents the increase in mean weight of the liver, with increase of length, in immature and non-pregnant female dogfish. The four curves refer to the four stations of the Fastnet group. They are distinguished by conventional signs explained in the figure. An inspection of the curves will show that they arrange themselves in such a way that the lowest curve is that for the Bantry Bay sample, the highest, the Outer Fastnet sample, in other words, the mean weight of the liver increases with increase of depth. This may also be demonstrated by using the coefficient k, as in the Table below, which has been extracted from Table XVIII.

Table VII.

Fastnet Group. Immature and Non-Pregnant Females. Liver.

Station.	Depth. Fathom.	50–59 cm. Mean length.	50–59 cm. Mean value of k (liver).	60–69 cm. Mean length.	60–69 cm. Mean value of k (liver).	70–79 cm. Mean length.	70–79 cm. Mean value of k (liver).
Bantry Bay	30	55·0	·0234	64·7	·0250	74·3	·0310
Galley Head	61	55·5	·0216	64·6	·0267	72·3	·0351
Inner Fastnet	89	58·5*	·0238*	65·8	·0321	73·1	·0355
Outer Fastnet	100	—	—	67 3	·0345	75·2	·0413

* Omitted in Figure 9.

In all three length-categories dealt with in the table, the value of k (liver) increases with increase of depth ; the only discrepancy is the value of the mean for 50–59 cm. in the Galley Head sample.

In Figure 10 are drawn the four corresponding curves for the mean weight of flesh in the stations of the Fastnet group. The flesh, like the liver, is seen to show a tendency towards an increase in mean weight with increase of depth, though this is not so well-marked as in the liver. The curve for Galley Head, in particular, is high, and the large fish at this station were heavier than the fish of corresponding size at either the Inner or the Outer Fastnet. In the table below are set forth the values of the coefficient k (flesh).

Table VIII.

Fastnet Group. Immature and Non-Pregnant Females. Flesh.

Station.	Depth. Fathom.	50–59 cm. Mean length.	50–59 cm. Mean value of k (flesh)	60–69 cm. Mean length.	60–69 cm. Mean value of k (flesh)	70–79 cm. Mean length.	70–79 cm. Mean value of k (flesh).
Bantry Bay	30	55·0	·289	64·7	·289	74·3	·290
Galley Head	61	55·5	·295	64·6	·297	72·3	·325
Inner Fastnet	89	58·5	·313*	65·8	·302	73·1	·299
Outer Fastnet	100	—	—	67·3	·287	75·2	·301

* Omitted in Figure 10.

The relation between depth and "condition" in the flesh can still be traced, but there is a discrepancy in the 60–69-cm. category, where the Outer Fastnet value is lower than the Inner Fastnet value, and in the 70–79-cm. category, where the Galley Head value is very high.

In Figure 11 are set forth the curves for increase in weight of the liver, with increase of length, in male dogfish in the four Fastnet stations. These curves show, even more clearly than those for the females, the increase in mean weight of the liver with increase of depth. There is one curious difference between males and females, however ; as Figure 11 shows, the curve for increase of weight with increase of length does not continue to rise, but falls away from the 60–69-cm. category to the 70–79-cm. category. This falling-off in the condition of the larger (and older) males may also be observed in the variations in the value of the coefficient k (liver).

Table IX.

Fastnet Group. Males. Liver.

Station.	Depth. Fathom.	50–59 cm. Mean length.	50–59 cm. Mean value of k (liver).	60–69 cm. Mean length.	60–69 cm. Mean value of k (liver).	70–79 cm. Mean length.	70–79 cm. Mean value of k (flesh).
Bantry Bay	30	57·2	·0179	66·5	·0240	72·8	·0235
Galley Head	61	56·8	·0221	66·0	·0278	72·7	·0275
Inner Fastnet	89	—	—	66·4	·0327	72·3	·0326
Outer Fastnet	100	—	—	67·5	·0317	72·2	·0365

There is only one exception to the otherwise perfectly demonstrated increase in mean weight with increase in depth ; this is in the 60–69-cm. category, where it is seen that the Outer Fastnet sample gives a low value of k (liver).

When the curves for increase of weight in the flesh, with increase of length, are drawn, an increase of mean weight with increase of depth is shown more definitely than in the female, though not nearly so well as

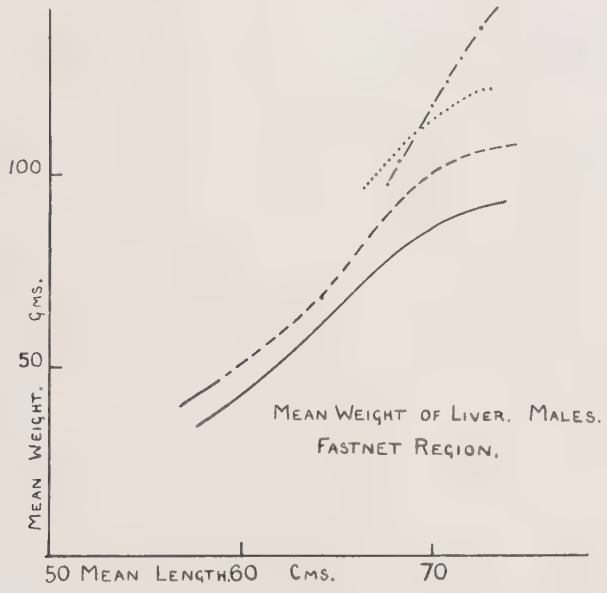

Fig. 11.—Fastnet Region. Curves showing increase in mean weight of liver, with increase of length, in male dogfish. *George Bligh*, August, 1928. Data from Table XVIII.

the liver in either sex. These curves are not shown in the text, since it is plain that the flesh does not share, to an extent comparable with the liver, in the curious agreement between depth and condition to which this section draws attention. The values of the coefficient k will be sufficient to indicate the variations in the condition of the flesh, with regard to depth.

When these variations, in the case of the males, are examined, as in the table below, it is seen that the Inner and Outer Fastnet samples, in the 60–69-cm. category, have lower values than the Galley Head sample, while, in the 70–79-cm. category, the Outer Fastnet value is lower than the Inner Fastnet value.

Table X.

Fastnet Group. Males. Flesh.

Station.	Depth. Fathom.	50–59 cm. Mean length.	50–59 cm. Mean value of k (flesh).	60–69 cm. Mean length.	60–69 cm. Mean value of k (flesh).	70–79 cm. Mean length.	70–79 cm. Mean value of k (flesh).
Bantry Bay	30	57·2	·283	66·5	·281	72·8	·276
Galley Head	61	56·8	·287	66·0	·292	72·7	·285
Inner Fastnet	89	—	—	66·4	·287	72·3	·298
Outer Fastnet	100	—	—	67·5	·290	72·2	·287

In summing up the deductions to be drawn from this examination of the data from the Fastnet region, it may be said that the liver, in both males, and in immature and non-pregnant females, shows a striking agreement with depth, such that the weight of the liver increases with increase of depth. This increase may be shown both by an inspection of the actual mean weights, and by using the length-weight coefficient k. The flesh shows this relation to a much slighter degree, especially in the deeper water.

When the males are compared with the immature and non-pregnant females, it is found that both liver and flesh in the female are slightly heavier, at any given depth, than in the male. This may be shown conveniently by using the coefficient k, as in the table below.

Table XIa.

Fastnet Group. Liver in Males and Females Compared.

Station.		Depth. Fathom.	50–59 cm. Mean length.	50–59 cm. Mean value of k (liver).	60–69 cm. Mean length.	60–69 cm. Mean value of k (liver).	70–79 cm. Mean length.	70–79 cm. Mean value of k (liver).
Bantry Bay	♂	30	57·2	·0179	66·5	·0240	72·8	·0235
	♀		55·0	·0234	64·7	·0250	74·3	·0310
Galley Head	♂	61	56·8	·0221	66·0	·0278	72·7	·0275
	♀		55·5	·0216	64·6	·0267	72·3	·0351
Inner Fastnet	♂	89	—	—	66·4	0327	72·3	·0326
	♀		—	—	65·8	·0321	73·1	·0355
Outer Fastnet	♂	100	—	—	67·5	·0317	72·2	·0365
	♀		—	—	67·3	·0345	75·2	·0413

Fastnet Group. Flesh in Males and Females Compared.

Bantry Bay	♂	30	57·2	·283	66·5	·281	72·8	·276
	♀		55·0	·289	64·7	·289	74·3	·290
Galley Head	♂	61	56·8	·287	66·0	·292	72·7	·285
	♀		55·5	·295	64·6	·297	72·3	·325
Inner Fastnet	♂	89	—	—	66·4	·287	72·3	·298
	♀		—	—	65·8	·302	73·1	·299
Outer Fastnet	♂	100	—	—	67·5	·290	72·2	·287
	♀		—	—	67·3	·287	75·2	·301

The exceptions to the above, in the case of the liver, are in the 50–59-cm. and 60–69-cm. category in the Galley Head sample, and the 60–69-cm. in the Inner Fastnet sample. In the case of the flesh, the only exceptions are

the Outer Fastnet values at 60–69 cm., in which the male is slightly heavier than the female. The table justifies one, in my opinion, in stating that the liver and flesh of the female dogfish tend to be heavier, at any given depth, than the liver and flesh of the male.

Hitherto, we have only considered immature and non-pregnant females. In the Fastnet group of stations sufficient numbers of pregnant females to be worth discussing were only found at the Bantry Bay and Galley Head stations. As Table VI shows, pregnant females in the Bantry Bay sample (30 fathoms) had both liver and flesh considerably lighter than in the Galley Head sample (61 fathoms). In this series of stations, therefore, pregnant females show the same increase in mean weight, with increase of depth, shown by immature and non-pregnant females, and by males.

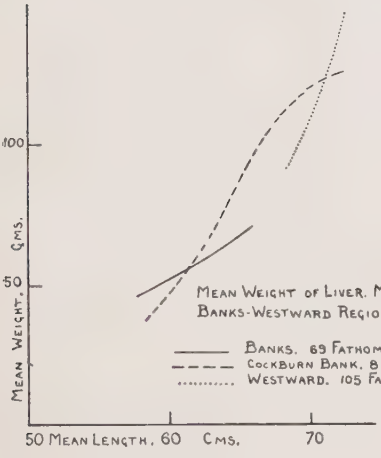

Fig. 12.

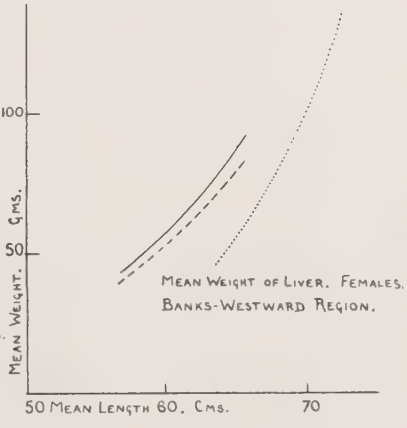

Fig. 13.

Figs. 12 and 13.—Banks-Westward Region. Curves showing increase in mean weight of liver, with increase of length, in male (Fig. 12) and female (Fig. 13) dogfish. *George Bligh*, August, 1928. Data from Table XVIII.

These results, based on the well-sampled Fastnet group of stations, confirm, by an inspection of the 10-cm. categories, the conclusions, based on the mean values of all specimens, drawn from Tables IV and V; they may now be compared with the Banks-Westward, and Galway-Bull groups of stations.

A comparison of the mean weights of liver and flesh at the three stations in the Banks-Westward group of stations is difficult, because, as we have seen in Section I, larger fish, especially females, are rare or absent in the Banks and Cockburn Bank samples, while smaller fish are lacking in the Westward sample.

In Figure 12 are drawn three curves, distinguished by conventional signs, representing the increase of mean weight of the liver of male dogfish,

with increase of length, in the three stations of the Banks-Westward series. The curves do not lie parallel to one another, and do not show the same increase in mean weight, with increase of depth, shown by the fish in the Fastnet region. The curves for the shallowest (Banks), and the deepest station (Westward), are continuous with each other, while the curve for the Cockburn Bank sample cuts both, showing the same falling-off at the higher-length category shown by the males in the Fastnet stations.

In Figure 13 the corresponding three curves for the females are drawn. Here there is a definite relation between mean weight and depth, but it is the reverse from what was found in the Fastnet region. Here, the mean weight of the liver decreases with increase of depth.

In the table below are set out the values for the coefficient k in both liver and flesh, for both sexes, in the three stations of the Banks-Westward region.

An inspection of this table shows that the relation between depth and condition in the liver tends to be an inverse one, especially in the female, whereas the flesh tends to show a direct correlation between depth and condition.

TABLE XIB.

BANKS-WESTWARD GROUP. BOTH SEXES. LIVER.

Station.		Depth. Fathom.	50–59 cm. Mean length.	50–59 cm. Mean value of k (liver).	60–69 cm. Mean length.	60–69 cm. Mean value of k (liver).	70–79 cm. Mean length.	70–79 cm. Mean value of k (liver).
Between Banks	♂	69	58·0	·0238	64·6	·0237	—	—
	♀		57·1	·0237	65·0	·0317	—	—
Cockburn Bank	♂	81	58·3	·0187	64·8	·0307	71·2	·0343
	♀		56·5	·0218	63·9	·0279	76·0	·0171
Westward	♂	105	—	—	68·5	·0288	72·5	·0381
	♀		—	—	63·5	·0177	76·5	·0454

BANKS-WESTWARD GROUP. BOTH SEXES. FLESH.

Between Banks	♂	69	58·0	·261	64·6	·257	—	—
	♀		57·1	·277	65·0	·246	—	—
Cockburn Bank	♂	81	58·3	·268	64·8	·300	71·2	·305
	♀		56·5	·297	63·9	·294	76·0	·296
Westward	♂	105	—	—	68·5	·319	72·5	·279
	♀		—	—	63·5	·258	76·5	·319

When the values of k (liver) and k (flesh) in males and females are compared, as in the table above, it is apparent that, in some cases, the liver and flesh are heavier in the male than in the female, while, in other cases, the reverse is true. Thus, the male liver is lighter than the female liver in the Cockburn Bank sample at 50–59 cm., in the Banks sample at 60–69 cm., and in the Westward sample at 70–79 cm. The male flesh is lighter than the female flesh in the Banks, and Cockburn Bank samples

at 50–59 cm., in none of the samples at 60–69 cm., and in the Westward sample at 70–79 cm.

Thus, neither the increase in mean weight of the liver, with increase of depth, nor the greater mean weights of liver and flesh in the female, are definitely confirmed by the Banks-Westward samples, and, though the data available from these are inadequate for a comparison with the Fastnet samples, they must be borne in mind, especially the reversal of the depth-weight relation in the females in the Banks-Westward region.

In the Galway-Bull group, a profitable comparison is only possible as between the pregnant females, since males of a size greater than 50 cm. were practically absent from all three stations, and immature and non-pregnant females were absent from the Galway Bay sample, and from the sample from very shallow water inside the Aran Islands. It may be pointed out, however, that, as Table V shows, immature females have a very high value of k (liver) (·0409) in the Bull sample (130 fathoms). This is also true of the flesh.

Comparing the pregnant females in Table VI from the station inside the Aran Islands (21 fathoms) with those from the Galway Bay station (55 fathoms), it can be seen that the flesh of the pregnant females at these two stations is approximately equal, the liver distinctly lighter in the shallower station.

It should be interesting to compare the mean weight and the mean value of the coefficient k, in pregnant females from the Galway-Bull groups of stations, with the Fastnet and Banks-Westward groups of stations, because it was suggested, in the first section of this paper, from an examination of the length-distributions, that the three groups of stations showed, in the order named, a progressively later stage in the birth of the young. The comparison may be made by an inspection of Table VI.

The lowest value of k, in the flesh, is found in the Bantry Bay sample. The very shallow water station inside the Aran Islands, and the Galway Bay station, have values which, though equal to, or higher than those for Bantry Bay, are considerably less than those for Galley Head, and the Westward ground. The last-named stations have liver and flesh showing contrary tendencies. The liver in the Westward sample is considerably heavier than the liver in the Galley Head sample, but the flesh in the Westward sample is slightly lighter than the flesh in the Galley Head sample. But before the data in this table can be examined for confirmation, or the reverse, as to whether the process of parturition of the year's brood of young progresses from west to east, as suggested earlier in this paper, the liver and flesh in pregnant and non-pregnant females must be compared.

A direct comparison is possible at only two stations, namely, Galley Head, and the Westward, since the fish compared must be of approximately equal length.

In Table XIIa, below, are set out the mean weights, and the mean values of the coefficient k, in both liver and flesh, at these two stations, in the 80–89-cm. category.

Table XIIa.

Comparison of Liver and Flesh in Pregnant and Non-Pregnant Females. 80–89 cm.

Station.	Depth.	Mean length.	Mean weight (liver).	Mean value k (liver).	Mean weight (flesh).	Mean value k (flesh).
Galley Head, pregnant	61	83·3	192	·0334	1950	·337
non-pregnant		81·7	233	·0428	1730	·318
	Difference		−41	−·0094	+220	+·019
Westward, pregnant	105	84·5	215	·0353	1960	·325
non-pregnant		81·0	215	·0403	1800	·339
	Difference		0	−·0050	+160	−·014

Both stations agree in the following points : The liver of the pregnant female is lighter, having regard to the mean lengths, than that of the non-pregnant female, and the flesh of the pregnant female is heavier than that of the non-pregnant female. In the 70–79-cm. group, in the Westward sample, the liver is considerably lighter in the pregnant than in the non-pregnant fish, but the flesh is also lighter. As Table XVIII in the Appendix shows, the value of k (liver) is always low in pregnant females.

A voyage made on the Fleetwood steam-trawler *Kumu* in October, 1928, to the Inishtrahull grounds, off the north-west of Ireland, gave me a good opportunity to compare the mean weight of liver and flesh as between non-pregnant females, females early in pregnancy, and females late in pregnancy. As in Ford's November samples at Plymouth, there were three groups of embryos at this time. There were large embryos, from 22 to 27 cm., smaller embryos from 7 to 10 cm., and, finally, very young embryos still enclosed in their horny capsules. The female dogfish were divided into three classes, namely, non-pregnant females, females containing horny capsules, and females containing embryos of the two larger sizes. The length-category 80–89 cm. was chosen for the comparison, which is made in the table below.

Table XIIb.

Inishtrahull. October, 1928. Comparison of Condition in Females 80–89 cm.

Female category.	Mean length.	Mean wt. of liver.	Mean value of k (liver).	Mean wt. of flesh.	Mean value of k (flesh).
1. Non-pregnant	81·9	238	·0433	1625	·296
2. Pregnant (Capsules)	83·8	232	·0391	1810	·308
3. Pregnant (Embryos)	86·0	167	·0261	1945	·305

In comparing the non-pregnant females (row 1) with the pregnant females containing embryos (row 3), exactly the same relation between the two classes is shown, as has been described in the Galley Head and Westward samples. The liver is considerably lighter in pregnant than in non-pregnant females, the flesh decidedly heavier.

In the pregnant females containing capsules, that is, in an early state of pregnancy, the liver is only slightly lighter than the liver of non-pregnant females, but the flesh is already decidedly heavier. Thus one may suggest that the liver is gradually drained of its resources during pregnancy ; but the increase of weight of the flesh may be due to a development of the musculature to cope with the extra work involved during the long period of pregnancy.

Returning to Table VI, it is seen that, although the Bantry Bay sample has the lowest k value of liver and flesh, the two stations in the Galway-Bull group have lower combined k values of liver and flesh than the two stations in the Fastnet group, and may therefore probably show a more advanced state of pregnancy in the females, subject to the qualification set out in the following paragraph.

On the other hand, Table XIIA also shows that the difference between the mean weights of the liver and flesh in pregnant and non-pregnant females is much less in the Westward than in the Galley Head sample. In the dogfish samples obtained on the voyages of the *Florence Brierley*, there was no difference between the mean values for k (liver) in pregnant and non-pregnant females. The mean value of k (liver) in the pregnant females was ·042, identical with that for the non-pregnant females. These fish were all taken in very deep water, and it may therefore be possible that the greater part of the weight of the liver lost by the pregnant females may be lost during the actual inward migration from deep to shallow water.

During the 1928 cruise of the *George Bligh* I made a note that the liver of the embryo dogfish appeared remarkably creamy and full, almost filling the body-cavity. During the 1929 cruise, I was able to make some experiments to test this.

The modal length of the embryos found in Galway Bay was 21 cm., and the first mode of free-living young was at 29 cm. The value of k (liver) in the embryos at the modal length (mean of 9 specimens) was ·033, in the free-living young (mean of 15 specimens) ·025. Thus, from an investigation of an admittedly small number of fish, the conclusion seems to be confirmed that the liver in the embryo is very much heavier, relatively, than the liver in the newly-born fish, and that the very rapid growth which seems to take place immediately after birth may be at the expense of the material stored in the liver. Reach (1912) finds that, in Torpedo, the embryo collects reserve fat in the liver, at the expense of the yolk.

During the exploratory voyages for Hake organised by the Fleetwood

Fishing-Vessel Owners' Association, in March, April, and May, 1927, I was able to make some weighing experiments on Dogfish at times when this fish was being caught, but when Hake were few or absent. The liver only was weighed. The results were read at the meeting of the British Association (Section D) at Leeds, in August, 1927. Owing to the fact that the data were too scanty to be grouped in 10-cm. categories, the mean value for the coefficient k in all the fish in the sample is used. Full data are given in the Appendix, Table XIX. The results are shown in Figure 14.

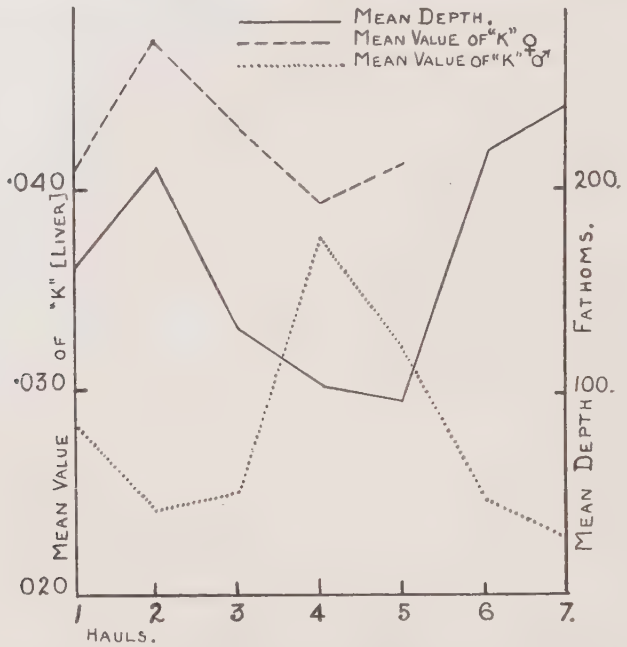

FIG. 14.—Curves showing the correlation between mean depth, and mean value of k (liver), in males and females. *Florence Brierley*, April, 1927. Data in Table XIX.

The numbers along the abscissa are the serial numbers of the hauls, in the order in which they were made in the Faroe-Shetland Channel. These numbers may be compared with the numbers in the Appendix,* from which the details of the hauls may be gleaned. The ordinates represent the mean value of the coefficient k (liver) (scale on the left), and the mean depth of haul (scale to right).

Three curves are drawn. The continuous line represents the mean depth, the pecked line the mean value of k (liver) in the females, and the dotted line the mean value of k (liver) in the males.

There is a direct coincidence between the mean value of k (liver) and the

* Table XIX.

depth of haul in the female, and in this respect the work on the *Florence Brierley* confirms well the results of the *George Bligh*. A second point in which the two sets of experiments confirm one another is in the much smaller mean weight of the liver in the male as compared with the female. Where they differ entirely is in the relation between the mean value of k (liver) and the mean depth of haul, in the males. Whereas in the experiments on the *George Bligh* we found that the mean weight of the liver increased with increase of depth, in the experiments on the *Florence Brierley* the reverse was true, and there was a strikingly good inverse

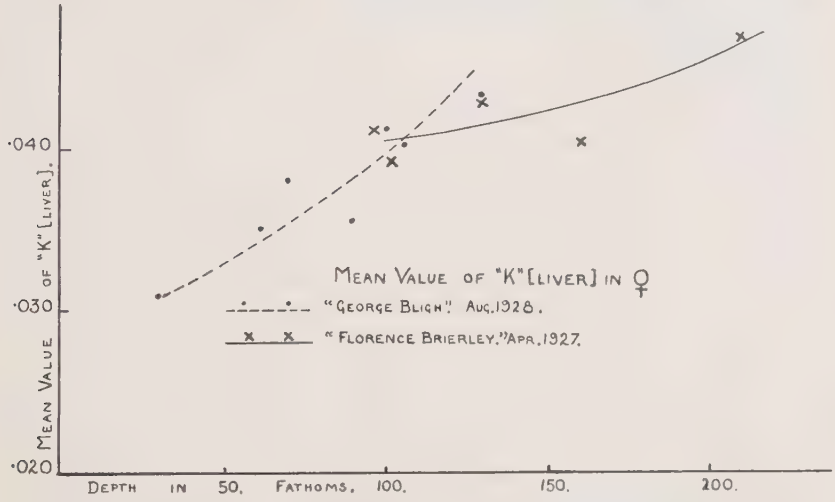

FIG. 15.—Curves drawn roughly through the plotted points for increase in mean value of k (liver), with increase of depth. Females. *George Bligh* and *Florence Brierley*. Data in Tables XVIII and XIX.

relation between the mean depth of haul and the mean value of the coefficient k (liver).

In Figure 15 free-hand curves are drawn through the plotted points for mean value of k (liver) in the immature and non-pregnant females from the *George Bligh* series of observations (black dots), and from the *Florence Brierley* series (crosses). As the table in the Appendix shows, the mean length of the females in the *Florence Brierley* samples varied between 74·7 and 83·9 cm., hence they have been compared with the length-category 70–79 cm. in the *George Bligh* series. A further point to notice is, that, in the *Florence Brierley* samples, pregnant and non-pregnant females have not been distinguished ; but, as has been stated, there was no difference in the mean value of k (liver) in pregnant and non-pregnant females.

Figure 15 shows that the two series of samples give free-hand curves

which are very similar and reasonably continuous. The curve derived from the *Florence Brierley* samples is decidedly flatter than that derived from the *George Bligh* samples, but one may say that, on the whole, the *Florence Brierley* samples, which continue into deeper water than the *George Bligh* samples, also continue the upward slope of the curve for mean value of the coefficient *k* (liver).

In Figure 16 are drawn the corresponding curves for males in the two series of samples. As in the females, the males in the *Florence Brierley* samples are compared with the males of 70–79 cm. in the *George Bligh* samples, since the males in the former have a range in mean length of 70·3 to 74·6 cm., or very similar to that of the males of 70–79 cm. in the *George Bligh* samples.

Owing chiefly, no doubt, to the difficulty of assigning a correct mean

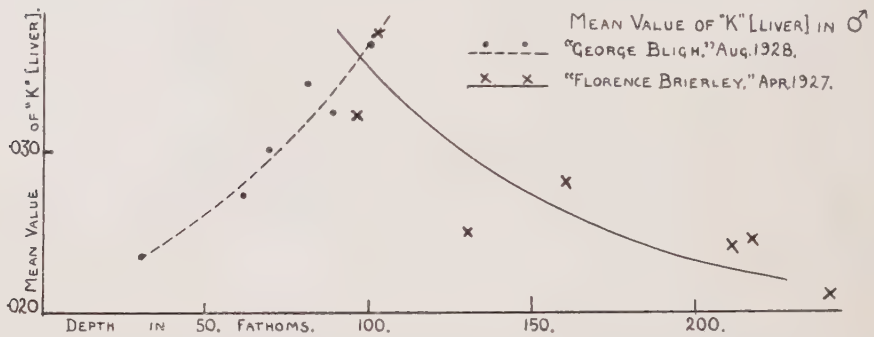

FIG. 16.—Curves drawn roughly through the plotted points for increase in mean value of *k* (liver), with increase of depth. Males. *George Bligh and Florence Brierley.* Data in Tables XVIII and XIX.

depth of haul to the hauls made on the slope, which is very steep beyond 150 fathoms in the Faroe-Shetland Channel, the plotted points for the *Florence Brierley* males are scattered somewhat irregularly as compared with the *George Bligh* males. None the less, where the depths worked by the two expeditions meet, at 90–110 fathoms, their plotted points are in good agreement, and the two curves are wholly comparable.

Figure 16 therefore shows that, in male dogfish, the mean value of *k* (liver) increases, with increase of depth, to a depth between 90 and 110 fathoms. At depths greater than this, the mean value of *k* (liver) decreases with increase of depth.

In the first section it has been stated that, at or over very great depths, were found shoals of exclusively male dogfish ; these may certainly be regarded as having been taken in midwater during the hauling or shooting of the trawl. In my report on the fishes taken by the *Florence Brierley* (Hickling, 1928), I have shown that Acanthias was taken at

every depth fished, from 90–100 to 500–520 fathoms. At depths greater than about 250 fathoms, males alone were taken. Hjort (1912) records the finding of *Acanthias vulgaris* living pelagically over very great depths north of the Faroes. Hence it would appear that, possibly at all depths, and certainly over the very deep water in the region of the continental slope, the spur-dog can, and does, live pelagically.

Figures 15 and 16 should therefore be interpreted thus, in my view. The females are bottom-living to a greater extent than the males, and, while it is possible that, as indicated, perhaps, by the flattening of the curve, in Figure 14, beyond 100 fathoms, they become to some extent pelagic in deeper water, the males certainly do so beyond this depth, and, from this depth toward deeper water, tend to live more and more pelagically, that is, for an increasingly large proportion of the fish to have been taken at depths intermediate between surface and bottom. This would explain the progressive decrease in mean weight of the liver in the males, with apparent increase of depth, beyond about 100 fathoms; it is entirely consistent with the curious segregation of males alone in, or over, very deep water. But this will be touched on again in the discussion.

DISCUSSION.

As a result of the study of the length-distributions of the dogfish at the various stations, it was concluded that (1), the fish are segregated according to size in such a way that the smaller fish are found in shallower, the larger in deeper water; (2) the males are found in shallower water than the females of the same size; and (3) the pregnant females make a migration into shallow water, passing through the shoals of dogfish of smaller sizes, to bear their young.

This graduation according to size is well known among fishes. Thus, Meek (1916) writes, of fish in general, "after a period in relatively shallow water, and this period is generally the summer, the shoal migrates to deeper water. At first, the migration is not to a great distance, but with growth the annual pulsation becomes greater and greater." Of the Spur-dog he writes, "the young of the species measure 22 to 25 cm., and they remain inshore during the summer. . . . They do not appear to migrate far from the coast in the first winter. The migrations are local during the phase of immaturity, and when the dogfish reach maturity, they tend to migrate into shallow water in summer, and to deep water for winter, keeping together in large companies."

Ford (*loc. cit.*) made notes on the composition of the dogfish shoals occurring off Plymouth. His samples were taken by fishing vessels, hence, as might be expected, he makes no mention of very small newly-born fish. From November 26th to July 29th his samples consisted of

" medium-sized fish, of which the majority were immature females," and " immature fish in which males and females were equal in number." The range in length seemed to be from 36 to 60 cm., and usually 40 to 60 cm. This is what one would expect in samples from shallow water. The inward migration of the pregnant females in the autumn is clearly indicated by his samples 11, 12, and 1, in August and early November. The withdrawal of the females after the birth of their young is indicated by the statement that " towards the end of November, it became noticeable that . . . the proportion of the conspicuously large fish was diminishing." Ford's conclusion that " Size and sexual condition are important factors in the constitution of the shoals in this species, the former probably being the more influential one," is also in entire agreement with my results, and I consider that the two sets of observations confirm one another in a very satisfactory way. His sample 2, from the catches of a steam-trawler, in which only 19·8% of females were present, can be explained by the assumption that she was fishing in a region where, as on the Cockburn Bank in our samples, males greatly predominated as a result of the segregation of the dogfish by size, and the concentration of the older year-classes of males at a certain depth, as explained earlier in this paper. The observation of Borcea (1905) that only females are found off Roscoff in the summer, is probably a further observation on the inward migration of the pregnant females. Quigley (1928), however, finds that the shoals of the Pacific dogfish " consisted of both sexes, and all sizes of fish, or else the ' baited set-line ' had been visited within a few hours by several different shoals." Especially significant is his observation that " the largest fish were usually taken at a greater depth than the smallest, and it may be that the composition of the shoals is in part determined by size."

The study of the variations in " condition " of the dogfish led to the conclusion that, although indefinite and even contrary results were found in the Banks-Westward region, there is, in the liver, and perhaps to a less striking degree in the flesh, a relation between depth and " condition " in males, immature females, and pregnant females. The " condition " improves from shallower to deeper water.

It should be emphasized that this is no mere " statistical figment " ; the work was commenced as a result of the obvious difference in size and oiliness between the livers of dogfish taken in deep, and shallow water, a difference most noticeable on dissection.

Polimanti (1915) investigated the fat-content of a number of fishes from a variety of habitats, and found that the fat-content decreased with increase of depth, in such a way that pelagic fish had the highest fat-content, and that bottom-living fishes had a fat-content decreasing as the depth of the habitat increased. Deep-sea fishes, of which, however. he

was able to analyse only one species, the bathypelagic *Cyclothone microdon*, had the lowest fat-content. He was of the opinion that a high fat-content supplements the swim-bladder as an agency of flotation, in fact, that the functional relations between the swim-bladder and the fat and water content are very intimate. He quotes the well-known relation between fat-content and vertical movement in fish eggs and larvæ, and also quotes those authors who have shown that, in Clupeidæ, there is a relation between fat-content and depth : in the summer they live at the surface, and are rich in fat, while in the winter they live in the depths, and are poor in fat.

In a paper to Section D of the British Association in 1927, I pointed out that, since the liver in the dogfish is known to consist largely of oil, a fish with a large liver must be relatively lighter, in relation to the water in which it swims, than a fish with a small liver. The liver, in fact, must act more or less as an organ of flotation, just as Polimanti suggested for fat in general among fishes.

During the 1928 cruise of the *George Bligh* I made direct determinations of the specific gravity of dogfish. The loss in weight on weighing the fish first in air, and then in sea-water, was used for calculating the specific gravity. The results are given in Table XX. The weighted mean value of k (liver) is also given for comparison. The specific gravities are the means of a good number of determinations in each case, made during the most favourable weather conditions. In Table XX the stations at which these determinations were made are arranged in order of depth.

Table XX.

Variations in Weighted Mean Value of k (liver), and in Specific Gravity. *George Bligh*, 1928.

		Male.		Female.	
Station.	Depth.	Weighted mean value of k (liver).	Mean specific gravity.	Weighted mean value of k (liver).	Mean specific gravity.
Inside Aran Islands	21	—	—	·0234	1·044
Bantry Bay	30	·0229	1·046	·0256	1·037
Galway Bay	55	—	—	·0265	1·036
Galley Head	61	·0266	1·040	·0303	1·038
"Station 18"	69	·0310	1·044	·0325	1·034
Outer Fastnet	100	·0340	1·043	·0407	1·037
Westward	105	·0350	1·040	·0359	1·040
Mean			1·043		1·038

Table XX shows in quite a striking degree the increase in the index of condition, with increase of depth, in both sexes. In the males, the specific gravity tends to decrease with increase of depth, but the females show no relation between the specific gravity and depth. It is possible, however, that the development of the very large eggs, and pregnancy, serve to discount the effect of local differences in the buoyancy of the

liver. None the less, the females have a consistently lower specific gravity than the males, which is in good agreement with their consistently heavier and larger liver. This seems to support the hypothesis that the condition of the liver affects the specific gravity.

Masterman (1911) reports on the specific gravity of the Plaice, and found that this decreases with increase of depth, especially in the females where it decreases from 1·077 at depths of less than 20 fathoms, to 1·068 at 30 to 40 fathoms. According to these experiments, in the Plaice, as in male dogfish, the fish are lighter, relatively to the water in which they swim, in deeper than in shallower water.

My observations are confined to weighings only, and no chemical analyses have been possible. But there is no reason to doubt but that the increase in the bulk of the liver, which takes place in the deep, as compared with the shallow water, is due to an accumulation of fat. Therefore my results contradict Polimanti's, except, perhaps, in the females of the Banks-Westward series, and in the males in the deep water of the Faroe-Shetland Channel, where the liver decreased in weight with increase of depth. But it is difficult to see how Polimanti's general conclusion can be upheld in the case of the deep-sea bathypelagic selachians. In *Scymnorhinus lichia*, for example, the liver is enormous: it fills the body-cavity, and may even protrude through the abdominal pores. The liver of this shark is very rich in oil. I have some data on the weight of the liver in the deep-sea selachian *Spinax niger*.

During a voyage on the Cardiff steam-trawler *Nogi* in January, 1928, I weighed the livers of 30 mature specimens of Spinax, ranging from 34 to 45 cm. in length. The mean value for the coefficient k (liver) was ·0736, and the weight of the liver amounted to 24% of the weight of the fish. The range in depth of Spinax, according to my observations on the *Florence Brierley*, is from 120 to 400 fathoms, and of Scymnorhinus from 220 fathoms to at least 520 fathoms (Hickling, 1928). Hence it is plainly incorrect to assume that deep-sea fish are poor in fat—indeed, among selachians, at least, the reverse seems true, for the highest mean value for the coefficient k (liver) in Acanthias was ·0409 (Bull, 130 fathoms), which is far less than the figure of ·0736 quoted above for Spinax.

Channon (1928) has analysed the liver oils from a considerable number of species of fish, and gives, in tabular form, the percentage of unsaponifiable matter in the oils. Of especial interest is his Table III, in which those members of the Selachii which he examined are arranged in order of decreasing content of unsaponifiable matter. It is plain that these fish are also arranged in decreasing order of depth. The deep-sea sharks Scymnorhinus, Lepidorhinus, and Spinax, have very high values, the shallow water sharks Lamna, Scyllium, and Galeus, have very low values for percentage of unsaponifiable matter; while Acanthias and Notidanus

have intermediate values. It seems reasonable to suggest that a modification in metabolism, with reference to depth, which takes place in the Selachii as a group, may also take place in a single species ; and that the increase in mean weight of the liver, with increase of depth, observed in Acanthias, may be due to an increasing quantity of unsaponifiable matter. The point will be tested, if opportunity offers.

We may now put side by side the main facts relating to the distribution of the dogfish on the one hand, and the condition, with especial reference to the liver, on the other.

(1) The fish are segregated according to depth, so that the smaller fish are found in shallower water, the larger in deeper water.

(2) The males are found in shallower water than the females of the same size.

(3) The pregnant females migrate from deep to shallow water to bear their young.

(1) The coefficient of condition in the liver is higher in larger than in smaller fish.

(2) The males have a lower coefficient of condition in the liver than the females.

(3) Pregnant females have a lower coefficient of condition in the liver than non-pregnant females, the difference increasing with decrease of depth.

When it is remembered that the coefficient of condition increases with increase of depth quite independently of the increase due to the greater mean length, these three pairs of facts fall surprisingly into line. The large fish have a higher coefficient of condition than the small fish, and are found in deeper water ; the females have a higher coefficient of condition than the males, and are found in deeper water than the males of the same size ; and, finally, the pregnant females are found to lose condition as they migrate from deep to shallow water.

On the other hand, we have seen that, in the Banks-Westward region, the dogfish were present in deeper water than those of the same size in the Fastnet region (Section I), yet, as Tables IV and V show, the mean values for the coefficient k (liver) are lower, not higher, in the Banks-Westward than in the Fastnet series.

It is not suggested that the " condition " is responsible for the distribution : it is hard to see how this could be the case. The only conceivable manner in which condition might affect the vertical distribution of the fish would be, as Polimanti suggested, by its effect on specific gravity. But dogfish with a lower specific gravity are found in deeper water, not in shallower water, as Polimanti's hypothesis demands. It might also be suggested that the inward migration of the pregnant females is due to the drain on the resources of the liver, causing a loss in condition, and therefore a movement into shallower water, but, in deeper water, the condition

of pregnant and of non-pregnant females differs only slightly, the difference, however, becomes progressively greater as the water becomes shallower. The "condition" would seem to be rather a consequence of the distribution, than a cause of it.

Borley (1912) found that there was a correlation between distribution and condition in Plaice, such that the smaller Plaice were in better condition in shallower water than in deeper water; the medium-sized Plaice were in better condition at intermediate depths than in either deep or shallow water; while large Plaice were in their best condition in deep water. He suggests that "grounds of different depth . . . are suitable to the nourishment of Plaice of different sizes, the size increasing with depth."

This hypothesis might be applied to the dogfish. If shallower water is better suited to the nourishment of small dogfish than deeper water, then they will tend to collect and remain in shallow water, and to be in their best condition there. In Figures 9 and 12, for instance, the curves tend to intersect so as to indicate that, although the larger fish in the samples have heavier livers in the deep than in the shallow water, among the smaller fish the reverse may be the case. Unfortunately, fish smaller than 50 cm. were not weighed. But the hypothesis would also have to explain the tendency for the males to be found in shallower water than the females of the same size, and to explain the loss of weight during the inward migration of the pregnant females.

Such notes as have been made on the stomach-contents of the dogfish do not support the idea that the deeper water provides more suitable food for the larger fish than the shallower water.

In the very shallow water stations inside the Aran Islands (21 fathoms) and in Bantry Bay (30 fathoms), the food consisted of herrings, small horse-mackerel, garfish (Belone), and whiting; in Galway Bay (55 fathoms) and off Galley Head (61 fathoms), herrings, mackerel, horse-mackerel, whiting, bib (*Gadus minutus*), "smelt" (*Argentina sphyræna*), and Eupagurus, were found in the stomachs; while on the Westward ground (105 fathoms), the food consisted of large horse-mackerel, blue whiting (*Gadus Poutassou*), and squids. The presence of herrings, mackerel, and garfish in the shallower water would seem to provide a richer fare than the large horse-mackerel, blue whiting, and squids in the deeper water.

Of course, a loss of condition can be the result of rapid growth in length, as well as of an environment less favourable to the nutrition of the fish. But if the poorer condition of the dogfish in the shallower water were due to their more rapid growth, one would expect that the fish in the shallower water would be larger than those in the deeper water, whereas the reverse is found.

The shoaling of the dogfish by size is easily understandable on Ford's

suggestion that it is more advantageous for fishes of the same size to congregate together, since, in shoals of fish of very varying sizes, it is probable that the small fish would suffer disadvantage, for instance, in their chances of obtaining food. The presence of the very small fish in shallow water is the consequence of their having been born there. But the persistence of the small fish in shallower water, and the very perfect graduation with depth according to size, calls for a special explanation.

A tentative modification of Borley's hypothesis is here suggested. It seems possible that depth itself involves some factor, or factors, tending to modify metabolism in the direction of greater storage of reserve material, and in an increase both in the proportion, and in the actual quantity, of unsaponifiable matter in the liver. The value of one unsaturated hydrocarbon, squalene, as a reserve material, is attested by its presence in the egg-oils of some Selachians. Heilbronn, Kamm, and Owens (1926) found that the young eggs of Spinax contained squalene, and that it was absorbed during the development of the embryo. Temperature may play its part, though the difference in temperature as between deep and shallow water is usually slight. However, in the deeper water there is a greater uniformity of temperature than in the shallower water. Pressure itself may be a factor of importance. This suggestion certainly derives some support from the hake, which retires to deep water during its exhaustion after spawning, and, in the conditions found there, makes a rapid recovery. (Hickling, 1930.)

As sexual maturity in the dogfish approaches, the fish tend to find the depth best suited to the accumulation of reserve material, rather than for growth alone, and thus, according to my hypothesis, seek deeper water. The more katabolic males, in which, in any case, the strain of reproduction is much less severe than in the females, will not need to seek such deep water as the more anabolic females, if the greater depths have an increasingly beneficial effect. Finally, the inward migration of the pregnant females carries them into depths less favourable to the replenishment of the reserve material, which is being withdrawn both to supply the energy for migration, and to nourish the young. There is thus a heavy loss in condition.

In this way, the " condition " might be the result of the distribution, and the distribution the result of the tendency of the fish to place itself in the most favourable conditions to satisfy its present metabolic needs.

While this hypothesis may go some way to meet the facts, it is always possible that the correlation of condition and depth may be dependant on some factors in the life-history of the fish, of which we are at present ignorant.

It may be added, finally, that the Spur-dog is a hardy fish, which would seem well suited to physiological experiments, and especially experiments on metabolism.

SUMMARY.

In August, 1928, dogfish were measured at a series of stations to the south, south-west, and west of Ireland. A relation was found between size and depth, such that the smaller fish were most abundant in the shallower water, the larger fish in deeper water. This relation was broken only by the pregnant females, fish generally over 80 cm. in length, which were in process of migration into shallow water to bear their young.

The male dogfish were present in shallower water than the females of the same size.

The sex-ratio varied with depth. In shallow water there was a slight predominance of females, at intermediate depths a predominance of males, and in deep water a gradually increasing predominance of females. This predominance of males at intermediate depths is liable to be masked by the inward migration of the pregnant females. [Over very deep water in the Faroe-Shetland Channel, in March, 1927, shoals of dogfish, consisting exclusively of mature males, were found.]

Weighing experiments were made both in the Faroe-Shetland Channel and off Ireland. The mean weight of the liver, and to a lesser degree, of the flesh, was greater in deep than in shallow water. That is, the fish were in better condition in the deep than in the shallow water. Exceptions were found both in the series of Irish stations and in the Faroe-Shetland Channel. [In the very deep water worked in the last-named region, the index of condition of the liver in the males decreased with increase of depth. It is suggested that this apparent progressive decrease in condition with increase of depth is actually due to an increasingly large proportion of the fish having been taken in midwater during the hauling and shooting of the trawl.]

The condition of the liver improves with increase of length, in both sexes : the livers of female dogfish are in better condition than those of male dogfish taken under the same conditions. Pregnant females lose condition during the migration from deep to shallow water. In the deep water they have an index of condition almost as high as non-pregnant females. Generally speaking, pregnant females have a lighter liver, but heavier flesh, than non-pregnant females.

These variations in condition are related to the distribution of the dogfish, but, in the discussion, it is concluded that the condition is the result of the distribution, rather than the cause of it, as Polimanti suggests. The better condition of the fish in deeper water is regarded as

due to an effect of depth, possibly pressure, on the metabolism of the fish, favouring anabolism rather than katabolism. Under the increased metabolic strain of maturity, the larger fish may therefore seek deeper water, the more anabolic females to a greater extent than the more katabolic males.

Female dogfish have a lower specific gravity than the males, in agreement with their larger liver.

The index of condition of the liver is much higher in Embryos than in newly-born dogfish, and it is suggested that a sudden spurt of growth takes place immediately after birth, at the expense of the material stored in the liver of the embryo.

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TABLE XIII.

MEASUREMENTS OF DOGFISH AT THE STATIONS. *GEORGE BLIGH*, AUGUST, 1928.

Upright figures denote frequency, italic figures denote percentage frequency.

	Banks—Westward Region.						Fastnet Region.											
Length in cm.	Banks 69 fathoms.		Cockburn Bank 81 fathoms.		Westward 105 fathoms.		Bantry Bay 30 fathoms.		Galley Head 61 fathoms.		Inner Fastnet 89 fathoms.		Outer Fastnet 100 fathoms.		Galway Bay 55 fathoms.		Station 18 69 fathoms.	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
25–	5	6	6	6			6	6	7	1					56	55		1
29	*3·6*	*5·2*	*4·0*	*2·5*			*1·2*	*1·7*	*1·6*	*0·4*					*12·3*	*16·0*		*1·1*
30–	47	21	32	18			239	139	47	31	1				268	205		
34	*33·8*	*18·4*	*21·5*	*7·3*			*47·1*	*39·8*	*10·8*	*11·3*	*0·2*				*58·9*	*59·6*		
35–	19	14	5	5			120	77	22	23					93	70	1	
39	*13·7*	*12·3*	*3·4*	*2·0*			*23·6*	*22·1*	*5·1*	*8·4*					*20·5*	*20·3*	*1·0*	
40–	17	6	9	6			61	53	9	6					28	13	3	
44	*12·2*	*5·3*	*6·0*	*2·5*			*12·0*	*15·2*	*2·1*	*2·2*					*6·2*	*3·8*	*3·1*	
45–	16	16	29	12		1	9	12	21	12	2				4	1	3	1
49	*11·5*	*14·0*	*19·5*	*4·9*		*9·1*	*1·8*	*3·4*	*4·8*	*4·4*	*0·5*				*0·9*	*0·3*	*3·1*	*1·1*
50–	14	25	16	22			15	6	36	23	8	2					11	3
54	*10·1*	*21·9*	*10·7*	*9·0*			*2·9*	*1·7*	*8·3*	*8·4*	*1·8*	*1·0*					*11·5*	*3·4*
55–	16	14	11	29			10	9	50	41	52	8	19				22	8
59	*11·5*	*12·3*	*7·4*	*11·8*			*2·0*	*2·5*	*11·5*	*15·0*	*11·6*	*4·2*	*5·3*				*22·9*	*9·1*
60–	2	6	19	48	2	1	9	9	52	42	135	34	51	4			25	9
64	*1·5*	*5·3*	*12·7*	*19·6*	*3·4*	*9·1*	*1·8*	*2·6*	*12·0*	*15·3*	*30·2*	*17·6*	*14·3*	*8·2*			*26·1*	*10·2*
65–	1	5	8	75	3	3	11	22	64	63	130	64	111	27			16	45
69	*0·7*	*4·4*	*5·4*	*30·6*	*5·2*	*27·3*	*2·2*	*6·3*	*14·7*	*23·0*	*29·1*	*33·2*	*31·0*	*55·1*			*16·7*	*51·2*
70–		1	4	23	7	6	9	15	47	28	75	73	95	16	1		7	18
74		*0·9*	*2·7*	*9·4*	*12·1*	*54·5*	*1·8*	*4·3*	*10·8*	*10·2*	*16·8*	*37·8*	*26·5*	*32·6*	*0·2*		*7·3*	*20·5*
75–			6	1	14		7	1	36	4	27	11	58	2			5	2
79			*4·0*	*0·4*	*24·1*		*1·4*	*0·3*	*8·3*	*1·4*	*6·0*	*5·7*	*16·2*	*4·1*			*5·2*	*2·3*
80–					19		7		25		13	1	18		2		2	1
84					*32·8*		*1·4*		*5·8*		*2·9*	*0·5*	*5·0*		*0·4*		*2·1*	*1·1*
85–	2		3		11		2		15		3		5		1		1	
89	*1·4*		*2·0*		*19·0*		*0·4*		*3·5*		*0·7*		*1·4*		*0·2*		*1·0*	
90–			1		2		2		3		1		1		2			
94			*0·7*		*3·4*		*0·4*		*0·7*		*0·2*		*0·3*		*0·4*			
Total	139	114	149	245	58	11	507	349	434	274	447	193	358	49	455	344	96	88
% ♀	54·9		37·8		84·1		59·2		61·3		69·8		88·0		56·9		52·2	
Medians	39·5	47·8	48·9	63·1	81·0	70·5	35·4	37·3	62·7	60·0	65·9	69·2	69·9	68·9	32·2	32·0	61·4	67·7

Table XIV.

Florence Brierley Dogfish. Faroe-Shetland Channel.

Date 1927.	G.M.T. of haul.	Mean depth. Fathoms.	Number of males.	Number of females.	Per cent of females.	Number of pregnant females.	Per cent of pregnant females.
March 25	1500	300	100	4	4	—	—
,, 27	0800	119	3	5	63	—	—
,, 28	1700	101	9	22	71	—	—
,, 28	2005	106	23	38	62	—	—
,, 29	0815	105	12	37	75	—	—
,, 29	1510	160	11	28	72	—	—
,, 29	1745	210	5	45	90	18	57
,, 30	1800	130	27	17	39	10	59
,, 31	1245	102	5	33	87	6	18
April 2	1930	96	10	35	78	4	12
,, 3	2115	216	41	0	0	—	—
,, 5	0800	240	24	2	8	2	100

Table XV.

August, 1929. Maturity of Male Dogfish. All Stations Combined. Based on Development of Claspers.

Length.	Numbers of Immature.	%	Mature.	%
52	21	100		0·0
53	10	100		0·0
54	9	100		0·0
55	10	90·9	1	9·1
56	10	90·9	1	9·1
57	8	72·7	3	27·3
58	4	66·6	2	33·4
59	7	58·3	5	41·6
60	4	33·3	8	66·7
61	4	26·6	11	73·4
62		0·0	12	100·0
63	1	4·5	21	95·5
64		0·0	23	100
65		0·0	11	100
66		0·0	17	100

Table XVI.

Onset of Pregnancy in Female Dogfish. All Stations, *George Bligh*, August, 1928.

Length Group.	No. of Females.	No. of Pregnant Females.	Per cent Pregnant.
55–59	—	0	0
60–64	44	1	2·3
65–69	41	1	2·4
70–74	49	6	12·2
75–79	29	6	20·7
80–84	49	33	67·4
85–89	35	31	88·6
90-94	11	10	90·9

Table XVII.

All Stations, *George Bligh*, August, 1928.

Frequencies of Embryos and Free-living Young.

Length.	Embryos.	Free-living Young.
18	1	
19	4	
20	13	
21	34	
22	48	
23	54	1
24	48	2
25	24	1
26	6	
27	2	14
28		34
29		106
30		191
31		264
32		244
33		195
34		142
35		94
36		94

Table XVIII.

George Bligh, August, 1928. Grouped Results of Weighing Experiments. Liver.

Station.	Depth. Fm.	50–59 cm. No. of speci-mens.	50–59 cm. Mean length.	50–59 cm. Mean weight of liver.	50–59 cm. Mean value of *h* (liver).	60–69 cm. No. of speci-mens.	60–69 cm. Mean length.	60–69 cm. Mean weight of liver.	60–69 cm. Mean value of *h* (liver).	70–79 cm. No. of speci-mens.	70–79 cm. Mean length.	70–79 cm. Mean weight of liver.	70–79 cm. Mean value of *h* (liver).	80–89 cm. No. of speci-mens.	80–89 cm. Mean length.	80–89 cm. Mean weight of liver.	80–89 cm. Mean value of *h* (liver).	90–99 cm. No. of speci-mens.	90–99 cm. Mean length.	90–99 cm. Mean weight of liver.	90–99 cm. Mean value of *h* (liver).
Banks	69																				
Males		13	58·0	47	·0238	12	64·6	66	·0237												
*Immature ♀		18	57·1	44	·0237	2	65·0	88	·0317												
Pregnant ♀																					
Cockburn Bank	81																				
Males		4	58·3	37	·0187	13	64·8	83	·0307	3	71·2	123	·0343								
*Immature ♀		5	56·5	39	·0218	12	63·9	73	·0279												
Pregnant ♀										2	76·0	75	·0171								
Westward	105																				
Males						2	68·5	93	·0288	4	72·5	145	·0381								
*Immature ♀						2	63·5	45	·0177	4	76·5	208	·0454	2	81·0	215	·0403				
Pregnant ♀						1	69·5	110	·0328	3	75·8	127	·0289	8	84·5	215	·0353				
Bantry Bay	30																				
Males		6	57·2	33	·0179	22	66·5	71	·0240	12	72·8	91	·0235								
*Immature ♀		16	55·0	40	·0234	14	64·7	67	·0250	14	74·3	129	·0310								
Pregnant ♀														10	83·9	128	·0222	2	92·5	203	·0257
Galley Head	61																				
Males		7	56·8	40	·0221	23	66·0	81	·0278	6	72·7	106	·0275								
*Immature ♀		10	55·5	38	·0216	22	64·6	73	·0267	13	72·3	135	·0351	6	81·7	233	·0428				
Pregnant ♀														9	83·3	192	·0334				
Inner Fastnet	89																				
Males						10	66·4	98	·0327	15	72·3	123	·0326								
*Immature ♀		2	58·5	48	·0238	15	65·8	93	·0321	10	73·1	140	·0355	5	82·9	280	·0486				
Pregnant ♀																					
Outer Fastnet	100																				
Males						16	67·5	98	·0317	14	72·2	139	·0365								
*Immature ♀						8	67·3	106	·0345	15	75·2	177	·0413	3	81·5	293	·0542				
Pregnant ♀																					
Inside Aran Islands	21																				
*Immature ♀																					
Pregnant ♀														5	84·9	156	·0261	3	92·8	125	·0156
Galway Bay	55																				
Males																					
*Immature ♀										3	74·2	109	·0264								
Pregnant ♀										3	76·5	101	·0227	25	85·3	165	·0266	5	92·1	211	·0270
Bull	130																				
Males																					
*Immature ♀						4	65·5	81	·0282	9	74·4	178	·0433	2	86·0	355	·0555				
Pregnant ♀														2	82·5	225	·0401				

George Bligh, August, 1928. Grouped Results of Weighing Experiments. Flesh.

Station.	Depth. Fm.	50–59 cm. No of speci-mens.	50–59 cm. Mean length.	50–59 cm. Mean weight of flesh.	50–59 cm. Mean value of *k* (flesh).	60–69 cm. No. of speci-mens.	60–69 cm. Mean length.	60–69 cm. Mean weight of flesh.	60–69 cm. Mean value of *k* (flesh).	70–79 cm. No. of speci-mens.	70–79 cm. Mean length.	70–79 cm. Mean weight of flesh.	70–79 cm. Mean value of *k* (flesh).	80–89 cm. No. of speci-mens.	80–89 cm. Mean length.	80–89 cm. Mean weight of flesh.	80–89 cm. Mean value of *k* (flesh.)	90–99 cm. No. of speci-mens.	90–99 cm. Mean length.	90–99 cm. Mean weight of flesh.	90–99 cm. Mean value of *k* (flesh).
Banks	69																				
Males		13	58·0	510	·261	12	64·6	700	·257												
*Immature ♀		18	57·1	520	·277	2	65·0	680	·246												
Pregnant ♀																					
Cockburn Bank	81																				
Males		4	58·3	530	·268	13	64·8	820	·300	3	71·2	1100	·305								
*Immature ♀		5	56·5	540	·297	12	63·9	770	·294												
Pregnant ♀										2	76·0	1300	·296								
Westward	105																				
Males						2	68·5	1030	·319	4	72·5	1060	·279								
*Immature ♀						2	63·5	660	·258	4	76·5	1490	·319	2	81·0	1800	·339				
Pregnant ♀										3	75·8	1317	·300	8	84·5	1960	·325				
Bantry Bay	30																				
Males		6	57·2	530	·283	22	66·5	830	·281	12	72·8	1060	·276								
*Immature ♀		16	55·0	480	·289	14	64·7	790	·289	14	74·3	1200	·290	10	83·9	1780	·301	2	92·5	2400	·304
Pregnant ♀																					
Galley Head	61																				
Males		7	56·8	530	·287	23	66·0	840	·292	6	72·7	1090	·285								
*Immature ♀		10	55·5	510	·295	22	64·6	810	·297	13	72·3	1240	·325	6	81·7	1730	·318				
Pregnant ♀														9	83·3	1950	·337				
Inner Fastnet	89																				
Males						10	66·4	840	·287	15	72·3	1130	·298								
*Immature ♀		2	58·5	630	·313	15	65·8	860	·302	10	73·1	1170	·299	5	82·9	1780	·312				
Pregnant ♀																					
Outer Fastnet	100																				
Males						16	67·5	900	·290	14	72·2	1080	·287								
*Immature ♀						8	67·3	870	·287	15	75·2	1290	·301	3	81·5	1700	·315				
Pregnant ♀																					
Inside Aran Islands	21																				
*Immature ♀																					
Pregnant ♀																					
Galway Bay	55													5	84·9	1920	·315	3	92·8	2330	·291
Males																					
*Immature ♀										3	74·2	1220	·297								
Pregnant ♀										3	76·5	1300	·291	25	85·3	1910	·307	5	92·1	2340	·299
Bull	130																				
Males																					
*Immature ♀						4	65·5	830	·295	9	74·4	1330	·320	2	86·0	2080	·356				
Pregnant ♀														2	82·5	1900	·339				

* Including non-pregnant females.

Table XIX.

Florence Brierley. April, 1927. Weighing Experiments.

	Haul.			Mean Depth.	Sex.	Mean Length.	No. of Specimens.	Mean value of k (liver.)
1.	March	29	1510	160	♀	74·7	27	·0407
					♂	70·3	12	·0284
2.	,,	29	1745	210	♀	83·9	31	·0470
					♂	74·6	5	·0242
3.	,,	30	1800	130	♀	83·9	17	·0430
					♂	72·4	16	·0252
4.	,,	31	1245	102	♀	75·1	32	·0393
					♂	72·4	5	·0376
5.	April	2	1930	96	♀	74·1	35	·0412
					♂	73·3	9	·0322
6.	,,	3	2115	216	♀	—	—	—
					♂	72·8	27	·0248
7.	,,	5	0800	240	♀	—	—	—
					♂	71·6	24	·0234

A Note on the Formation of the Egg Case of the Skate.

By

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With 2 Figures in the Text.

THERE seems to be some uncertainty about the exact stage at which the horny case is secreted around the fertilised Elasmobranch egg. Those textbooks which have been consulted either pass over the matter in silence or give the impression that the shell is secreted while the egg is passing through the nidamental organ. Sedgwick (1905), for example, says (p. 143) : " The shell is formed round the ovum and its albumen in the lower dilated part of the oviduct, but the material of which it is composed is secreted by the oviducal gland." Of late years the question seems to have received little attention, but there are several papers on the subject published twenty or more years ago.

Gerbe (1872) considered that in rays the albumen and shell are secreted simultaneously round the egg. He observed : " Un œuf à moitié engagé dans la glande, et qui possède une partie de son albumen, possède en meme temps une partie de sa coque."

Perravex (1884) investigated the structure of the nidamental organ of *Scyllium canicula* and discovered " dans une glande nidamenteuse de *Scyllium canicula* un œuf à demi engagé ; les cornes antérieures et la partie inférieure seules étaient formées. . . ." His conclusion was that, although secretion of the matter of which the shell is composed begins before the egg reaches the gland, yet the shell is actually formed around the egg.

Borcea (1904) concluded that formation of the shell begins before the egg reaches the nidamental organ on the ground that the pressure of the egg within the gland would prevent the secretion from passing between the lamellæ at the base of which the individual tubular glands open. He considered that " Le phenomène se passe d'une manière reflexe : l'œuf n'est qu'un stimulus qui le détermine." He did not, apparently, come across any specimens directly confirming his view, although he cited the occurrence of fully-formed egg cases containing only albumen as showing that the egg is not the only stimulus which can cause the secretion of a shell.

The most extensive paper on this subject is that of Widakowich (1906), who described the structure of the nidamental organ of *Scyllium canicula* in great detail and endeavoured to deduce the process of shell formation from his observations. He recognised that the caudal processes of the egg case are laid down during the passage of the egg down the part of the oviduct cranial to the nidamental organ. He thought, however, that the body of the case is formed during the subsequent movement of the egg through the gland. He found one specimen in which the anterior part of the egg case had not been completely formed, but here, apparently, the egg had already passed through the nidamental organ and was lying in the already fully-formed part of the case in the caudal region of the oviduct.

Beard (1890) stated that in skates, "It appears very likely, nay, almost certain, that the lower half of the purse is formed before the egg arrives at the oviducal gland, and that after the arrival of the egg the closure of the purse is at once effected." This conclusion, which is in complete agreement with the observations to be described in the present note, was based on the following circumstances. Firstly, "One often finds part of a purse in the oviduct and no yolk or egg within it." Secondly, about 10 per cent of some shark egg cases laid in captivity were found to contain no egg. It is unfortunate, with regard to the first observation, that it is not stated whether an egg was present in the oviduct.

It may be seen from the above references that, although intermediate stages in shell formation in Elasmobranchs have on several occasions been observed, there is a lack of precision in the descriptions which renders it difficult to draw definite conclusions as to the sequence of events in this process. Consequently, it is thought that the following observations may be of interest although they are based only on a single specimen of *Raia radiata* Donovan. Beard (1890) states that breeding specimens of this species are rare in the Firth of Forth. *Raia radiata* is now, however, the commonest species among those dissected in the Department of Zoology in the University of Edinburgh (*cf.* Lamont, 1926), and individuals containing egg cases are fairly plentiful.

Pregnant individuals almost invariably are found with one or two fully-formed and closed egg cases in the part of the oviducts posterior to the nidamental organ or in the vagina. Occasionally a specimen may be noticed in which the anterior horns of the cases are still within the nidamental organ. The exception to be described in which the egg cases are only half formed is the only one which has been noticed in such a condition among, at a rough estimate, 150 pregnant female skate of several species. This indicates that, once ovulation has taken place, the passage of the egg down the cranial part of the oviduct and the formation of the shell is accomplished quickly.

A general view of the specimen of *Raia radiata*, on which the following

observations are based, is seen in Fig. 1. The liver and alimentary canal have been removed in order to display the reproductive organs. The left ovary has been turned over towards the middle. Anterior to the nidamental organ (N.O.) each oviduct is swollen by a mature ovum (Od.) which is yet devoid of either white or shell. Behind the nidamental organ on either side the oviduct is greatly distended by the posterior half of the egg case (E.C.), whose vague outlines can be distinguished through the

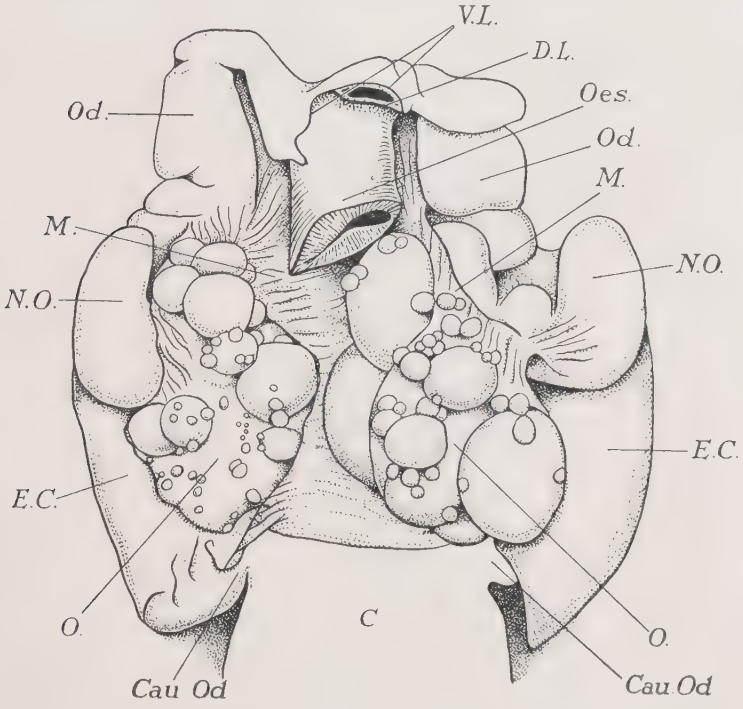

Fig. 1.—O., ovary; M., mesovarium; D.L., V.L., dorsal and ventral lips of oviducal funnels; Od., ovum in cranial part of oviduct; N.O., nidamental organ; E.C., egg case in caudal part of oviduct; Cau. Od., undistended part of caudal oviduct; C., cloaca; Oes., œsophagus. (Nat. size.)

oviducal wall. Behind the egg case each oviduct is at liberty to retain its normal diameter and turns sharply towards the middle line to join that of the other side to form the cloaca (C.). Fig. 2 shows the condition of the egg case. The ventral half of the left nidamental organ and of the oviduct immediately posterior to it has been removed. The egg case (E.C.) can be seen lying in the distended part of the caudal oviduct. At O.U. is the opening into the yet undistended part of the oviduct. About half of the egg case has already been formed. Its only difference from the final product is that it is lighter in colour and somewhat softer. Widakowich

(1906) has pointed out that the case of *Scyllium canicula* is formed by a large number of separate elements (" Platten ") which adhere to each other comparatively loosely at first but later, and especially after contact with sea-water, much more closely so that the whole shell hardens.

The half-formed egg case is quite empty. Its dorsal and ventral walls are well separated from one another so that at the anterior end there is an opening which will admit the egg when it is ready to pass into the case. It is probable, however, that the egg has to undergo a certain amount of distortion during this process.

It is evident that this specimen confirms the opinions expressed by

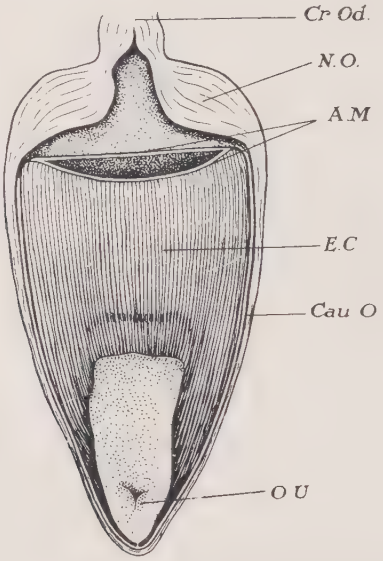

Fig. 2.—Ventral half of left nidamental organ and part of caudal oviduct removed to show half-formed egg case *in situ*. (×2.)

Cr. Od., cranial part of oviduct; N.O., nidamental organ; Cau. O., caudal part of oviduct; O.U. opening into undistended part of caudal oviduct; E.C., egg case; A.M., anterior margin of egg case.

Beard (1890) and by Borcea (1904), although neither of these workers presented critical evidence in favour of their views. At least half, and possibly considerably more, of the egg case is already formed before the egg comes into contact with the nidamental organ at all. Various authors (e.g. Perravex, Widakowich) have described the presence of shell material already secreted in the tubules of the shell gland before the egg has even been shed from the ovary. It is probable, therefore, that the shell gland commences activity some time before ovulation occurs The scarcity of observations between this period of preparation and the fully-formed

egg case with the egg enclosed, suggest that once the egg has reached the oviduct, events move rapidly.

It is a familiar fact that two ova are shed from the ovaries simultaneously, so that in each oviduct there is an egg in the same stage of development. In the specimen here described it may be noted that both eggs appear to have been shed from the right ovary. In Fig. 1 it can be seen that in the left ovary are several eggs in an advanced stage of development, whereas in the right ovary the largest eggs present are only about half-grown. This may indicate an alternation in the activity of the ovaries. Many further observations would be needed to establish this, but if it should prove to be generally true, it may readily be seen how, from such a condition, that found in *Scyllium canicula*, for example, could be derived, in which only one ovary develops and becomes functional.

One further point is illustrated in Fig. 1. In textbooks the oviducal funnels of both the skate and the dogfish are described and figured as being united to form a single median ostium. In *Raia radiata*, at any rate, this seems not to be the case. The upper and lower lips of the funnels are, indeed, united, but the openings remain so widely separated as to be, probably, functionally distinct. Redeke (1898) stated that in *Trygon pastinaca* there are two separate ostia (quoted by Ihle, 1927, p. 745). *Raia radiata*, therefore, seems to exhibit a condition intermediate between this and the completely fused ostia of *Raia batis*.

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The Preservation of Fishing Nets by Treatment with Copper Soaps and Other Substances. Part II.

By

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This paper is a continuation of Part I in a strict sense, and deals with the methods and samples considered previously. More prolonged immersion tests have enabled a more accurate estimate to be reached as to the relative values of the methods of preservation. One new preservative has been tried, an oily substance sold as "Neo-Russigen," a sample of which was supplied by the Ministry of Fisheries: in the absence of any chemical analysis of this there is no guarantee that subsequent supplies will approximate to the sample received, to which alone must the data presented be considered to apply.

The tables are completed or continued from Part I, and bear the numbers by which they were designated in Part I, to which reference as to the methods of treatment should be made. Table 14 is the only new one. In the tables more weight should be attached to the life of the net than to the percentage life, taking the untreated net as 100; this is because an untreated net placed to rot in October experiences cold weather and may last as long as five months, whereas if the immersion dates from early summer the warm weather results in more rapid decay and it may only last two months. The preserved nets will however go through both summer and winter. It might be better to take three months as a standard time for the rotting of untreated nets, but this varies also with the thickness of the twine, so the observed values have been given in each case.

A correction must be mentioned as regards the results shown in Table 7, Part I. Sample 51A, treated with the copper soaps and tar mixture, was rejected in error after eleven months. In reality it lasted for twenty months, but this is decidedly lower than usual with the mixture, cp. No. 14A, 39 months, No. 39A, over three years.

TABLE 3.

Hemp net rotting in Aquarium tank water; initial strength, average of sets of six, 13½ and 14¾ lbs. dry; after soaking for three hours, 12½ lbs. Immersed 26/9/'25.

No.	Treatment.	Till unserviceable, months.	Percentage life of net.
10	Untreated	5	100
11	Copper soaps, 12%, viz. 1 lb. per gal.	9	180
12‡	Do. with resin 1 lb. per gallon (12%)	11	220
13	Do. with anti-fouling paint, 12%	29*	580
14	Do. with tar, 12%	36†	720

‡ The soap and resin, paint or tar respectively were mixed, so that only one dip was required, 1 lb. of each being added to the gallon of copper soap solution in petrol.

* Half-strength after 26 months, still serviceable, looked as new.

† Slightly under half-strength after 26 months, still serviceable, looked as new.

TABLE 5.

Cotton net rotting in Aquarium tank water; initial strength, dry, 19½ lbs. Immersed 26/9/'25.

No.	Treatment.	Till unserviceable, months.	Percentage life of net.
10A	Untreated	5½	100
11A	Copper soaps, 12%	10¼	190
12A	Do. with resin 1 lb. per gallon (12%)	26*	470
13A	Do. with anti-fouling paint, 12%	37†	670
14A	Do. with tar, 12%	39‡	710

* Strength 10 lbs. after 25 months.

† Strength 17½ lbs. after 36 months.

‡ Strength 18 lbs. after 36 months.

TABLE 9.

Hemp net rotting in Aquarium tank water; initial strength, dry, averages of sets of six tests each, 15¼, 15¾, 18½; maximum single strand 21, minimum 12½ lbs. Immersed 17/3/'26.

No.	Treatment.	Life of net. Months.	Percentage.
28	Untreated	2½	100
29	Cutch, 2% infusion, two boilings	6	240
30	Do. followed by Olie's ammonia copper sulphate	30*	1200
31	As 29, followed when dry by 12% copper soaps	30*	1200
32	Copper soaps, 12%, but soaked for 3 hrs.	19	760
33	Copper soaps, 12% with 1 lb. resin per gallon	13½	540
34	Copper soaps, 12%, followed when dry by No. 33 treatment	29*	1160

* After 20 months strengths were 8 lbs., about half-strength.

TABLE 10.

Cotton net rotting in Aquarium tank water; initial strength, dry, 12 lbs. Immersed 17/3/'26.

No.	Treatment.	Life of net. Months.	Percentage.
24A	Untreated	2	100
26A	Cutch, 2% infusion, two boilings	3	150
25A	Do. followed by Olie's ammonia copper sulphate	5	250
27A	As 26A, followed when dry by 12% copper soap	5	250
28A	Copper soap, 12%, soaked for 3 hrs.	5	250
29A	Do. with 1 lb. resin per gallon	5	250
30A	As 28A, followed when dry by 29A treatment	25*	1250

* Strength 12½ lbs. after 19 months, all colour gone and strength 7½ lbs. after 20 months.

TABLE 11.

Cotton net rotting in Aquarium tank water; initial strength, dry, 18 lbs. Immersed 20/10/'26.

No.	Treatment.	Re-treatments.	Strength, after years. 1	2	3
34A	Untreated. Life 5½ months	None	0	0	0
35A	Cutch, two boilings	Every two months	16·3	0	0
36A	Do.	Every three months	18	9·8	4·6
37A	Do. followed by Olie's ammonia copper sulphate	Every four months	22·5	20·9	18·8

TABLE 12.

Hemp net Nos. 35–39 rotting in Aquarium tank water; Nos. 40-44 in fresh water. Immersed 25/11/'26. Initial strength, dry, 16½ lbs.

No.	Treatment.	Strength, after years. 1	2	3
35	Copper soaps, 12%. Life 14 months	5·3	0	0
36	Do. with tar as No. 14	14·3	11·4	7·5
37	Cuprinol with equal volume of petrol	12·3	8·3	4·8
38	As No. 37 with 1 lb. tar per gallon of mixture	16·3	12·3	13·1
39	Copper soaps as No. 35, Cuprinol as No. 37, equal volumes of each	13·0	10·1	5·8
40	As No. 35	7·0	7·4	5·3
41	As No. 36	9·0	9·1	6·6
42	As No. 37. Life 25 months	14·0	7·9	0
43	As No. 38	13·5	11·3	13·6
44	As No. 39	12	9·6	7·7

TABLE 13.

Cotton net Nos. 38A–42A rotting in Aquarium tank water; Nos. 43A–47A in fresh water. Immersed 25/11/'26. Initial strength, 18½ lbs., done on 40A before treatment, 17½ lbs. done on 45A similarly.

No.	Treatment.	Strength, after years. 1	2	3
38A	Copper soaps, 12%. Life 21 months	22	0	0
39A	Do. with tar as in 14A	18	17	18
40A	Cuprinol with equal volume of petrol	25	26	18
41A	As No. 40A with 1 lb. tar per gallon of mixture	25	22	19
42A	Copper soaps as 38A, Cuprinol as 40A, equal volumes of each. Life 30 months	25	13½	0
43A	As 38A	22	17	16
44A	As 39A	21	20	14
45A	As 40A	16½	20	21
46A	As 41A	21	19	22
47A	As 42A	26	21	25

TABLE 14.

Cotton net rotting in Aquarium tank water. Immersed 28/4/'28.

No.	Treatment.	Life of net. Months.	Percentage.
52A	Dipped in Neo-Russigen. Initial strength 11 lbs.	14	700
54A	Cutch, two boilings. Initial strength 12 lbs.	4½	220
55A	Untreated. Initial strength 11 lbs.	2	100

Discussion of Results.

Tables 3 and 5 show how great is the advantage of adding 1 lb. tar to the copper soaps mixture, 1 lb. to the gallon of petrol. Nets, hemp and cotton lasted up to or over three years when thus treated. The results shown in Tables 12 and 13, Nos. 36 and 39A confirm this. The degree of preservation achieved is undoubtedly very good, No. 39A having its initial strength after the three years. The results with anti-fouling paint were not quite as good as with tar; it is more expensive and the proprietary paints vary greatly. It is also far more messy than tar mixed in copper soap.

Tables 12 and 13 compare the British product, mixed copper soaps (stearate, palmitate, and oleate), with the Danish "Cuprinol," the copper soap of a naphthenic acid (or acids) derived from petroleum, probably Galician. Comparisons were made with and without tar, in both fresh and salt water. Both types of copper soap are more effective on cotton than on hemp. In sea-water Cuprinol is far more durable than is the

fatty acids soap. The two are about equal on cotton in fresh water, but on hemp the advantage lies with the fatty acids soap. The fresh water was the Plymouth tap supply, a very soft water with scarcely a trace of lime in it. When both are mixed with tar, Cuprinol and the fatty acids copper soap appear to be about equal, and the latter is very much the cheaper. Both give excellent preservation to cotton nets for three years under soakage conditions. With hemp Cuprinol shows up better than the fatty acid soap ; the latter is the product developed by Lever Bros. and later supplied as Pilot Protective Copper Soap by Messrs. Ogston and Tennant, of Renfrew. The results may probably be taken as applicable without serious error to the copper oleate, manufactured according to the American formula by Messrs. Wm. Bailey & Son, of Wolverhampton. It was, however, found (Atkins, 1926) that a 5% solution of the mixed soaps was just as effective as 10% of the pure oleate and it is possible that the former is more effective because of a lesser solubility. With tar such differences should be reduced, and the oleate is rather more readily soluble in petrol.

Table 14 shows that Neo-Russigen is much better than cutch alone, though not as good on cotton as fatty acid copper soaps, cp. No. 38A, but better according to No. 11A. It falls far behind copper soap and tar, however.

Tables 9 and 10 make a comparison of cutch and Olie's ammonia copper sulphate with copper soap. All the results are poor on the cotton of Table 10, except copper soap followed by copper soap with resin. On the hemp of Table 9, however, the preservation was good, Olie's method and copper soap after cutch coming out equal. Undoubtedly a preliminary treatment with cutch greatly enhances the preservative effect of both Olie's method and the copper-soap method.

It seemed advisable to test whether good preservation could be obtained by repeated treatments with cutch at two or three month intervals and of Olie's method at four-month intervals. Table 11 shows that three-monthly re-treatments with cutch are better than two-monthly, also that, under the test conditions, four-monthly re-treatments with Olie's method result in the original strength having been maintained for three years, which is equivalent to one treatment with copper soap and tar or Cuprinol and tar. The nets boiled in cutch and treated with ammonia copper sulphate feel rather harsh to the hand and give a clean break in the tensile test. The nets have not the softness and pliability of those treated with copper soap with or without tar. Fillon (1925) speaks highly of Olie's method and prefers it.

SUMMARY.

1. The most efficient preservation for a single treatment is given by a mixture of copper soaps and tar, either :

(*a*) One pound of a copper soap of mixed fatty acids (Pilot Protective Copper Soap) dissolved in one gallon of petrol or gas-works benzol. This gives a 12% solution approximately, to which 1 lb. of tar to the gallon is afterwards added. (*b*) "Cuprinol" may be used instead of the fatty acid copper soap as in (*a*). Cuprinol may be used alone and is more effective than fatty acid copper soap in sea-water; it is also more expensive. It is, however, improved, especially for hemp nets, by the addition of tar, 1 lb. to the gallon of mixed Cuprinol; the latter is sold as a solution, to be mixed with an equal volume of petrol before use. Hemp and cotton nets treated according to methods (*a*) and (*b*) have lasted three years when allowed to soak in Aquarium sea-water, in jars, the water being changed three times a week.

2. Efficient preservation, with maintenance of the original strength for three years, has also been given to cotton nets treated according to Dr. Olie's method and re-treated every four months. This treatment consists of boilings in cutch on two occasions, the net being dried in between. It is then soaked for 15 minutes in a 1% solution of copper sulphate* to which ammonia has been added in an amount just sufficient to re-dissolve the precipitate first formed.

I am indebted to my laboratory assistant, Mr. F. J. Warren, for performing the tensile tests during the last year.

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—— 1928. The preservation of fishing nets by treatment with copper soaps and other substances. *Loc. cit.*, **15**, 219–235.

Fillon, R. 1925. Les traitements préservateurs des filets de pêche en coton. Office sci. et tech. des pêches maritimes. Notes et mém., No. 45. Paris.

* One pound dissolved in ten gallons of fresh water, with about six ounces by weight of strong ammonia.

An Instrument for Sampling Marine Muds.

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and

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With 5 Figures in the Text.

This instrument was designed for taking marine muds for analysis. The requirements were that it should raise a column of mud, from eight to sixteen inches long, and without appreciable disturbance, or contamination with metal. An instrument working on the same principle was used here by Mr. R. Macdonald, and was made in Oslo. The advantages of the present model are that, while small enough to be worked by hand, it is capable of taking larger samples, and from bottoms of very varying consistencies.

Essentially it is a heavy brass body containing a glass tube, the latter being open at both ends when descending, so that the water may stream through it. The sampler falls under its own weight, and drives deeply into the mud, which partially fills the glass tube. A valve at the top closes when the sampler stops, and by this, and by its own friction against the glass, the mud is held in the tube while the sampler is hoisted. The overall length of the machine is 35 inches, the greatest diameter $3\frac{3}{4}$ inches, and the weight 35 pounds.

Glass tubes of three different diameters are used, to cope with the varying nature and holding capacity of the ground.

The instrument is shown assembled in Fig. 1, while Fig. 2 shows the details of the valve region. Fig. 4 is a horizontal section of the instrument. The main body is a heavy brass tube (Fig. 4, B), closed at the top by a brass plate, in which is a circular aperture ; the lower end is open, but has a projecting flange, threaded externally to take a lock-ring. The main tube or body is 9·57 inches long ; the plate at the top is 0·38 inches thick, and the body has an overall length of 9·95 inches. The aperture in the top of the plate is one inch in diameter. The walls of the body are 0·79 inches thick, and its external diameter is 3·75 inches.

The sheath (Fig. 4, D) into which the glass tube is loaded is a tube of ·075 inch brass, 14·8 inches long, and 2·15 inches in external diameter.

Five inches from the top is a heavy flange which fits against the bottom of the body. At its lower end the sheath is turned in to the extent of ·15 inch, to give protection to the bottom of the glass tube. The sheath is clamped to the body by a brass lock-ring (Fig. 3, c) which screws on to the bottom of the body. The ring and sheath are removed when inserting or withdrawing the glass tube.

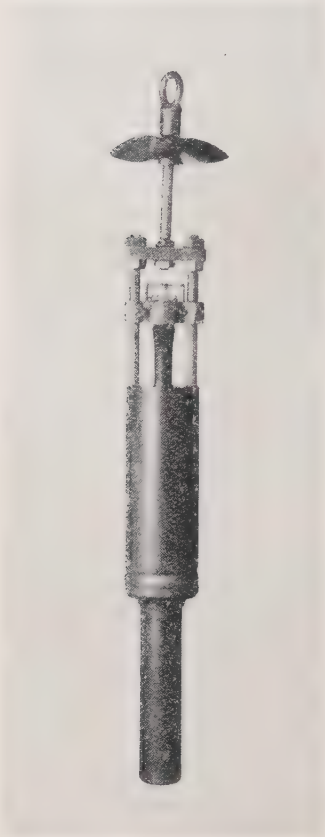

Fig. 1.—Photograph of bottom sampler.

Two brass rods (Fig. 4, a), 7·45 inches long and 0·63 inches in diameter, rise from the top of the body and support the valve mechanism, which is described below; to the link which unites them at the top is attached the central rod that bears the propeller. This shaft is 8·4 inches long, and carries at the top a ring for the attachment of a rope. The propeller itself revolves freely on the shaft, and is fitted to ensure straight descent. It has four blades, with a distance from tip to tip of six inches.

The glass tubes and their rubber connections are not shown in Fig. 4. For the sake of clearness, they have been displaced to the right, and are shown as Fig. 5. The shaded areas represent rubber, the unshaded glass. The glass sampler tube is 1·85 inches in external diameter, 0·1 inches thick, and 18·25 inches long: it lies within the sheath, and extends almost to the top of the body. The dimensions of these tubes vary slightly owing to the difficulty of obtaining uniform supplies. The bottom of the glass tube is open; the top receives a rubber bung, which must be tight-fitting. This is pierced for a small glass tube, 3·5 inches long, and just under an inch in external diameter, which passes through the aperture in the top plate of the body, and is connected by a rubber sleeve with the actual valve. The rubber bung, in addition to making the joint, serves to take up some of the shock, if, as sometimes happens, the sampler strikes a stone on the bottom. For the same reason it has been found desirable to adjust the bung so that the larger glass tube is not actually in contact with the turned-in bottom of the sheath. The glass tube is

held as rigidly as is necessary, when the bung is sufficiently tight-fitting to ensure the essential water-tight joint.

The valve is a glass tube, 2·25 inches long and slightly less than one inch in external diameter. Near the bottom it has a swelling to allow the

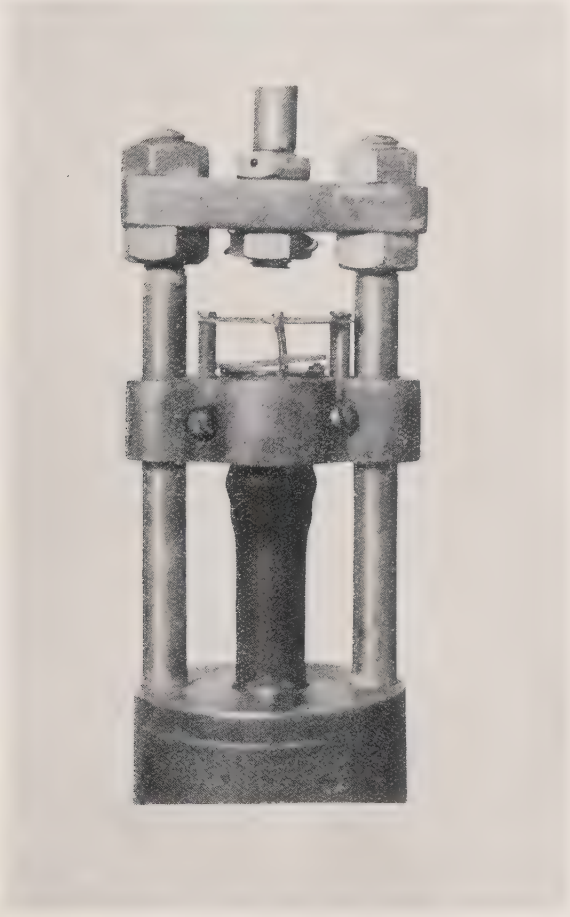

Fig. 2.—Photograph of valve region of bottom sampler.

sleeve to grip it. At the top it is turned over to form a rim about a quarter of an inch wide, and the upper surface of this rim is ground. On it lies a circular ground glass plate, confined only by the small cage shown in the figures. As the sampler descends, the water streams through the tube, and escapes through the valve, the ground glass plate being lifted by the pressure of the water. But as soon as the sampler comes to rest in the

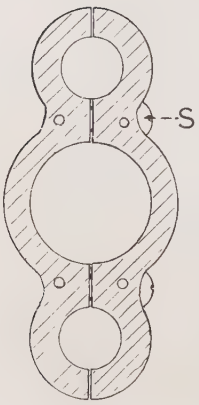

Fig. 3.—Plan of valve bar, $\times \frac{1}{2}$.

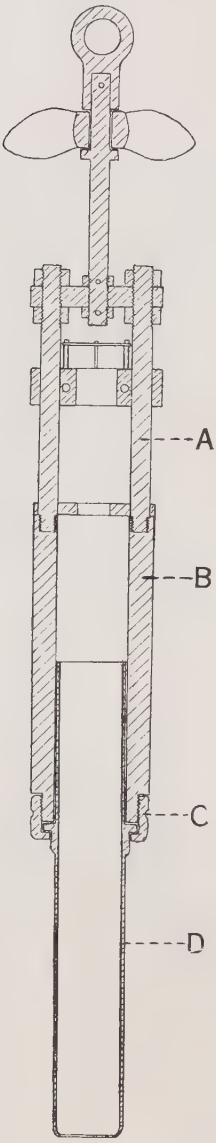

Fig. 4.—Diagram of bottom sampler, $\times \frac{1}{6}$: for lettering see text.

Fig. 5.—Glass parts of bottom sampler.

mud, the plate drops on to the ground rim beneath it, making a water-tight joint.

The valve carrier is shown in plan in Fig. 3. It consists of a split bar, 1·2 inches deep, which slides on the two uprights previously referred to : it is cut away in the centre to accommodate the valve. Two screws (Fig. 3, s) serve to clamp the two halves to each other, and to the supporting rods. Thus the valve is accessible, and its distance from the main body can be varied if necessary.

The length of the column of mud taken varies with the nature of the mud itself, and with the diameter of the glass tube with which the sampler is working. Sandy muds hold only in the medium or small tubes, and some clayey muds also hold badly owing to their slipperiness. The longest samples are usually taken in the 1·5 inch tubes. It is essential that all connections between rubber and glass should be good, or the muds will slip out. The instrument was designed to take three sizes of tubes, with external diameters of 2·0, 1·5, and 0·95 inches respectively. The figures show only the largest tube in position, but there are three interchangeable sheaths, one to fit each size of tube. They are all the same length, and the flange which the lock-ring grips is the same diameter in each. The assembly is the same with the 1·5-inch tubes as with the large ones, but with the smallest tubes there is this difference, that the tube itself is about three inches longer than the others, and projects through the aperture in the top of the body of the instrument, connecting directly to the valve by the rubber sleeving, the 3·5-inch tube, and the bung being dispensed with.

The instrument has now been in use at the Millport Laboratory for some months, in depths ranging from 10 to 70 fathoms, and has proved very satisfactory. With the 2-inch tubes, samples 12 inches long have been taken from depths of 60 fathoms, and the 1·5-inch tubes frequently give 16-inch samples. Whilst it has been designed for use with muds only, shorter samples of sands have been taken successfully with the small tubes.

The fauna of the muds can be seen well through the glass tubes. Whilst crustacean larvæ, etc., have been taken swimming in the water immediately over the mud, many burrowing molluscs and polychæts have been taken, as well as crustaceans and ophiuroids on some grounds. One interesting catch was a specimen of *Calocaris macandreæ*, taken in its burrow eight inches below the surface, at a depth of 35 fathoms.

The mud is raised without contamination, as it is never in contact with anything but glass. That it is raised without appreciable disturbance is shown by the fact that layers of different types of mud are often visible in the same sample, with very clear boundaries. Also there is very little disturbance of the fine upper layers.

After the tubes have been removed from the machine, the mud is

pushed out of them with a ramrod. A certain amount of breakage occurs with the glass tubes, and also the valves, so that it is well to have a reserve supply. It is often found most convenient to bring the mud back in the tubes, in which case spare ones are necessary. When ordering these it is advisable to specify that they shall be straight, as our first supply included some that were curved to such an extent that they would not enter the sheaths.

The instrument probably could be most profitably worked from a wire, but in our case it has proved more convenient to work it from a rope ; and we found that the speed of descent was quite sufficient with a 2-inch rope, even when working in depths of over 70 fathoms.

The Muds of the Clyde Sea Area.
1. Phosphate and Nitrogen Contents.

By

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With 5 Figures in the Text.

The Clyde Sea Area is in many ways an ideal ground for the investigation of the nutrient salts in the bottom deposits. The different lochs present a range of depth of water of from 0 to 200 metres: some parts have strong tidal currents up to five knots, while others are practically unaffected by the tide: some lochs have also been affected by the dumping of sewage and harbour sludge, and the effect of these can be examined. Conditions may also be compared in muds ranging from the loch heads to the almost open sea conditions at Ailsa Craig.

The fact that the mud is as nearly homogeneous as any bottom deposit can well be, coupled with the taking of eight or ten cores from each station, ensures the representative sampling of any region. Also, since cores of up to forty centimetres in length can be taken, the vertical distribution of the components of the mud may be examined.

A series of investigations is being made on the chemical, physical and geological nature of these muds, and on the relation of these to the fauna. The present paper deals only with their phosphate content, and their organic content as represented by total nitrogen. The organic content has not been estimated directly, as there is no accurate method that is applicable, whereas the nitrogen can be determined with great accuracy; further, the nitrogen content is of importance in giving a link in the chain of the nitrogen cycle in the sea. The results are tabulated, and then discussed.

This is only a preliminary statement, and it is hoped later to trace a connection between more of the factors concerned. In dealing with such a very complex set of conditions, and before drawing conclusions, it is necessary to take a sufficient number of stations to give significant results, and one must not apply them to a single station as a test of their truth. Irregularities are frequent, such as those due to the interpolation of a layer of sand at some level, and similar causes, but neglecting these cases, it is possible to see a certain amount of correlation between some of the factors in the area.

The muds in general are soft for the top ten centimetres or more, but rarely so soft, even at the very surface, as to form a so-called "Pea Soup" layer; they then become more clayey deeper down. The mud sampler, which is described in another paper (**3**), takes perfectly undisturbed samples, and shows that the surface of the mud is clearly marked off from the overlying water, with no contamination of the latter which would be clearly visible if present. It is not, however, the purpose of the present paper to discuss the physical character of the muds.

Although clear demarcation into layers is often present, no attempt has so far been made to analyse these natural layers separately. All samples taken are cut up on board the boat into five-centimetre lengths, and these are set aside in separate pots, to be taken back and dried as soon as possible. After drying at about 110° C. they are ground in an iron mortar and then passed through a 1 mm. sieve. They can then be stored in this condition in airtight jars until required.

Thirty-three stations have so far been worked, and their positions and depths are shown in the accompanying chart (Fig. 1). Wherever possible the stations have been those used by Marshall and Orr in their work on the plankton of the area (**1**).

Note on the Tides.

The chief points in the tidal streams, which vary greatly throughout the area, are given below. The figures refer to the maximum spring tides, and where two figures are quoted the first refers to the flood, and the second to the ebb tide. Up the Kilbrennan Sound (Arran Basin, west branch) the tide is about $2\frac{1}{2}$ knots, though greater in some shallows. In Loch Fyne the average tide is 2 knots, with an increase to $3\frac{1}{2}$ and $5\frac{1}{2}$ at the Otter Spit just north of St. 6, and $2\frac{1}{2}$ and 4 at the Minard Narrows: at St. 4 it has dropped to $1\frac{1}{4}$ and $1\frac{3}{4}$. The stream up the east coast of Arran is $1\frac{1}{2}$ knots, and the branch of this up the Inchmarnock Sound and West Kyle has a maximum of $2\frac{1}{2}$ knots. St. 7 has practically no tide, and there is very little in Loch Riddon (L. Ridun): at the top of the East Kyle there is a tide of 3 knots, but Rothesay Bay and Loch Striven have very little indeed.

To the east of Cumbrae the tide is 2 knots, and to the west, $1\frac{1}{2}$ knots. In the Dunoon Basin it is about 1 knot, rising off Gourock to 2 knots (St. 20a.) The Holy Loch, and Lochs Long and Goil have very little tide, but in the mouth of the Gare Loch there is a peculiar swirl, and a tide of up to 5 knots.

These figures of course refer to the surface currents, little being known of the bottom currents which directly influence the muds themselves. Further details with regard to the area may be found in Mill's "Clyde Sea Area" (**2**).

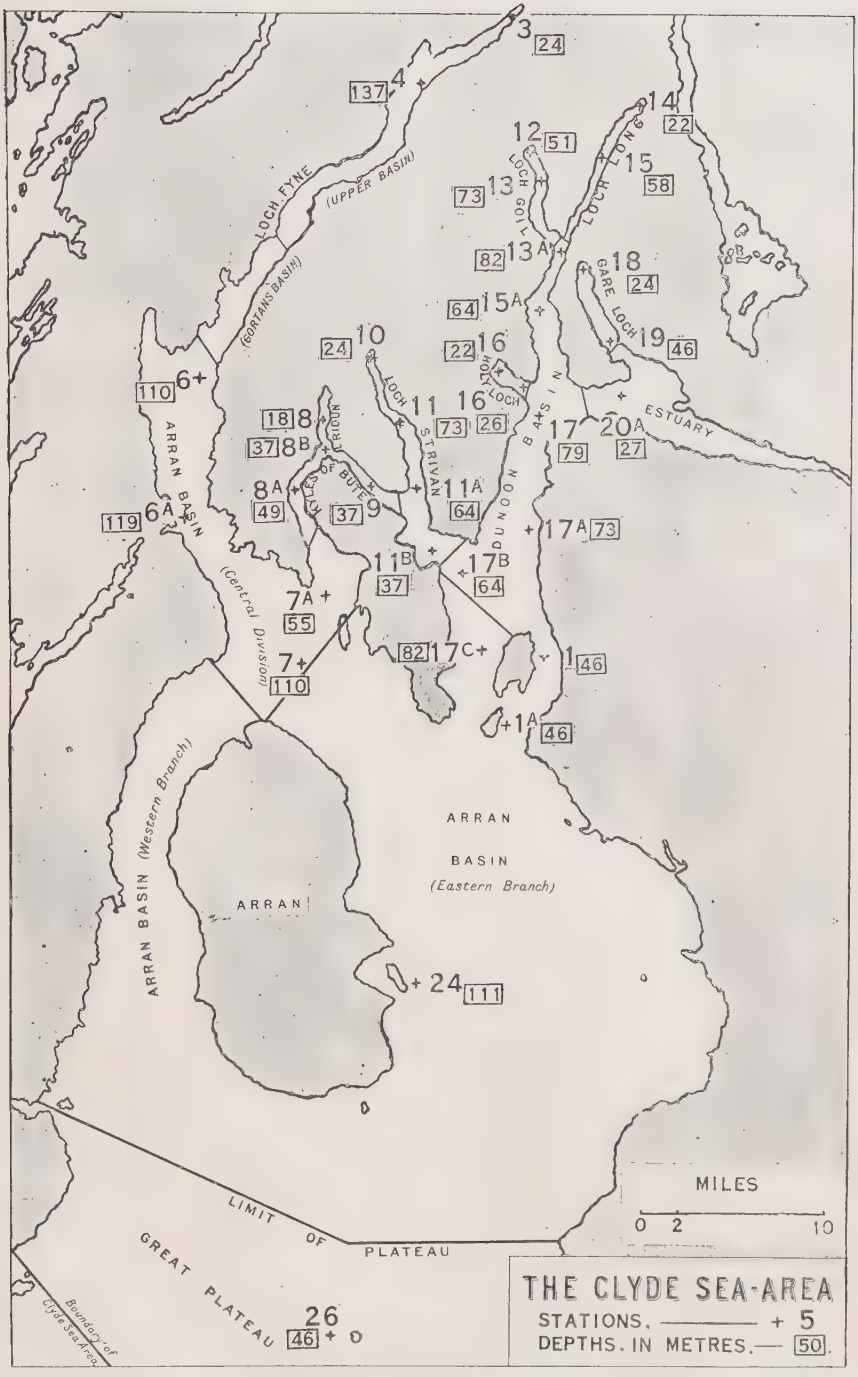
LOCH FYNE
(UPPER BASIN)
(GORTANS BASIN)
LOCH GOIL
LOCH LONG
GARE LOCH
ESTUARY
ARRAN BASIN
(Central Division)
KYLES OF BUTE
LOCH STRIVAN
DUNOON BASIN
ARRAN BASIN (Western Branch)
ARRAN
ARRAN BASIN
(Eastern Branch)
LIMIT OF PLATEAU
GREAT PLATEAU
Boundary of Clyde Sea Area
MILES
0 2 10
THE CLYDE SEA-AREA
STATIONS, ——— + 5
DEPTHS. IN METRES.— 50.

FIG. 1.

Phosphate Content.

Since any extract of the mud is very highly coloured, no colorimetric method of estimation of phosphate can be used; the most suitable method has been found to be that used in soil analysis, viz., of precipitation as ammonium phospho-molybdate, and solution of this in standard sodium hydrate solution, the excess of the latter being then titrated (**3** and **4**).

20 gm. of the dried mud are extracted for 48 hours with hydrochloric acid, in a water-bath, and the extract after filtering is made up to 250 c.c. Four portions of 25 c.c. are then taken from this for analysis. It has not been found necessary to compare with a known standard at each estimation, but each extract was estimated, as stated, four times for the sake of accuracy. The results for each station, at depth intervals of 5 cm., are given in Table I, together with a note of the general type of the mud and the depth of the water at each station.

TABLE I.

Phosphate Values expressed as Percentage by Weight of P_2O_5 in the Dried Mud.

M. = Mud. S.M. = Sandy Mud. S. = Sand.

Station.	Depth in Metres.	Type.	Depth in Mud in cm. 0–5.	5–10.	10–15.	15–20.	20–25.	25–30.
1	46	M.	0·244	0·195	0·187	0·175	—	—
1a	46	S.	0·152	0·145	0·142	0·142	—	—
3	24	S.M.	0·250	0·213	0·201	0·185	—	—
4	137	M.	0·270	0·220	0·240	0·216	—	—
6	110	M.	0·201	0·199	0·188	0·185	—	—
6a	119	M.	0·179	0·164	0·166	0·156	—	—
7	110	M.	0·214	0·177	0·180	0·169	—	—
7a	55	M.	0·169	0·156	0·142	0·149	—	—
8	18	S.M.	0·219	0·215	0·173	0·155	—	—
8a	49	M.	0·199	0·188	0·206	0·201	—	—
8b	37	M.	0·248	0·206	0·167	0·157	—	—
9	37	M.	0·237	0·203	0·229	0·201	—	—
10	24	M.	0·228	0·198	0·201	0·172	—	—
11	73	M.	0·226	0·206	0·220	0·204	—	—
11a	64	M.	0·266	0·188	0·219	0·216	—	—
11b	37	M.	0·219	0·178	0·177	0·185	0·170	0·175
12	51	M.	0·305	0·219	0·214	0·186	0·169	0·186
13	73	M.	0·406	0·219	0·239	0·211	0·207	0·203
13a	82	M.	0·284	0·266	0·230	0·226	0·236	0·200
14	22	M.	0·243	0·224	0·191	0·201	0·201	0·240
15	58	M.	0·328	0·321	0·289	0·266	0·299	0·253
15a	64	M.	0·241	0·209	0·261	0·228	—	—
16	22	M.	0·291	0·219	0·179	0·174	—	—
16a	26	M.	0·255	0·216	0·219	0·178	—	—
17	79	M.	0·267	0·228	0·198	0·087	—	—
17a	73	S.	0·149	0·142	0·109	0·099	—	—
17b	64	S.M.	0·215	0·187	0·209	0·183	0·182	0·197
17c	82	M.	0·200	0·181	0·181	0·172	0·156	0·152
18	24	S.M.	0·260	0·203	0·197	0·207	—	—
19	46	M.	0·364	0·298	0·263	0·284	—	—
20a	27	S.M.	0·168	0·189	0·185	0·141	—	—
24	111	M.	0·158	0·150	0·161	0·152	0·148	—
26	46	M.	0·117	0·101	0·129	0·119	—	—

Total Nitrogen Content.

As the various methods of organic content estimation are not of sufficient accuracy, whereas the total nitrogen can be estimated easily and very accurately, the latter estimation was chosen, and the ordinary Kjeldahl method used (**4**). Ten grammes of mud are taken for each estimation, and these are only duplicated when the results are suspected. The values found are given in Table II in the same form as those for the phosphates, the depths of water and types of mud being repeated for convenience.

TABLE II.

Nitrogen Values expressed as Percentage by Weight of N_2 in the Dried Mud.

M. = Mud. S.M. = Sandy Mud. S. = Sand.

Station.	Depth in Metres.	Type.	Depth in Mud in cm. 0–5	5–10	10–15	15–20	20–25	25–30
1	46	M.	0·189	0·170	0·165	0·181	—	—
1a	46	S.	0·099	0·101	0·097	0·083	—	—
3	24	S.M.	0·211	0·211	0·237	0·279	—	—
4	137	M.	0·304	0·279	0·232	0·209	—	—
6	110	M.	0·201	0·178	0·168	0·145	—	—
6a	119	M.	0·135	0·132	0·134	0·097	—	—
7	110	M.	0·183	0·167	0·162	0·161	—	—
7a	55	M.	0·089	0·083	0·074	0·074	—	—
8	18	S.M.	0·256	0·202	0·139	0·132	—	—
8a	49	M.	0·233	0·188	0·170	0·166	—	—
8b	37	M.	0·335	0·284	0·290	0·251	—	—
9	37	M.	0·219	0·201	0·195	0·194	—	—
10	24	M.	0·177	0·148	0·135	0·124	—	—
11	73	M.	0·238	0·237	0·211	0·204	—	—
11a	64	M.	0·262	0·245	0·223	0·211	—	—
11b	37	M.	0·137	0·153	0·132	0·146	0·114	0·114
12	51	M.	0·275	0·265	0·286	0·273	0·295	0·285
13	73	M.	0·379	0·291	0·267	0·237	0·260	0·250
13a	82	M.	0·257	0·198	0·167	0·211	0·242	0·210
14	22	M.	0·337	0·330	0·295	0·302	0·312	0·307
15	58	M.	0·268	0·271	0·231	0·172	0·216	0·188
15a	64	M.	0·242	0·208	0·206	0·202	—	—
16	22	M.	0·184	0·187	0·160	0·156	—	—
16a	26	M.	0·232	0·203	0·187	0·168	—	—
17	79	M.	0·208	0·255	0·221	0·212	—	—
17a	73	S.	0·069	0·051	0·043	0·041	—	—
17b	64	S.M.	0·229	0·204	0·205	0·178	0·180	0·177
17c	82	M.	0·195	0·201	0·176	0·174	0·167	0·160
18	24	S.M.	0·191	0·205	0·166	0·159	—	—
19	46	M.	0·221	0·285	0·158	0·163	—	—
20a	27	S.M.	0·208	0·123	0·150	0·099	—	—
24	111	M.	0·230	0·177	0·133	0·135	0·144	—
26	46	M.	0·119	0·116	0·111	0·102	—	—

Discussion of Results.

The results show that there is no general correlation of the depth of water with either the phosphate or nitrogen content of the mud in any layer, with the following exception. In the case of those shallow-water

stations less than forty metres, all the phosphate values lie close together, while covering a much wider range in the deeper stations. As in the case of most such linkages, the surface layers do not agree quite so well as the deeper layers where conditions seem to have become more stabilised. The distribution of P_2O_5 with depth of water for the 5–10 cm. layer, is shown in Figure 2, where the phosphate values for shallow

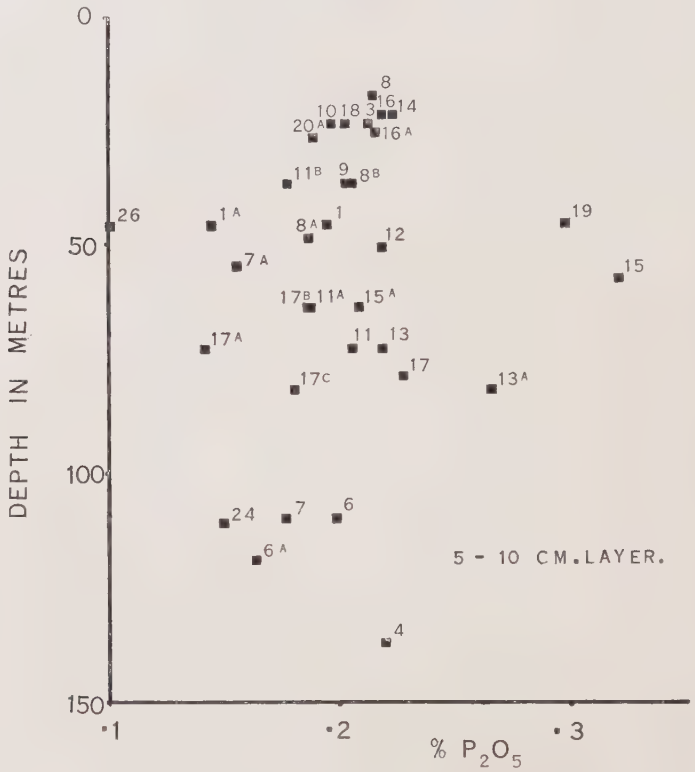

Fig. 2.—Graph showing the distribution of P_2O_5 with depth of water, in the 5–10 cm. layer throughout the area.

stations range only from 0·178% to 0·224%. In the case of the nitrogen content there does not seem to be such a correlation.

The distribution of phosphate with depth in the mud, throughout the area, is shown in Figure 3. The value falls with increasing depth in the mud in all but three stations in the whole area. These are St. 11b, 18 and 19, in all of which the value first drops and then rises again. The latter two stations are in the Gare Loch, which is a backwater into which much fine silt from the river is carried, forming a thick layer all over the bottom. (Mill, p. 646, 2.)

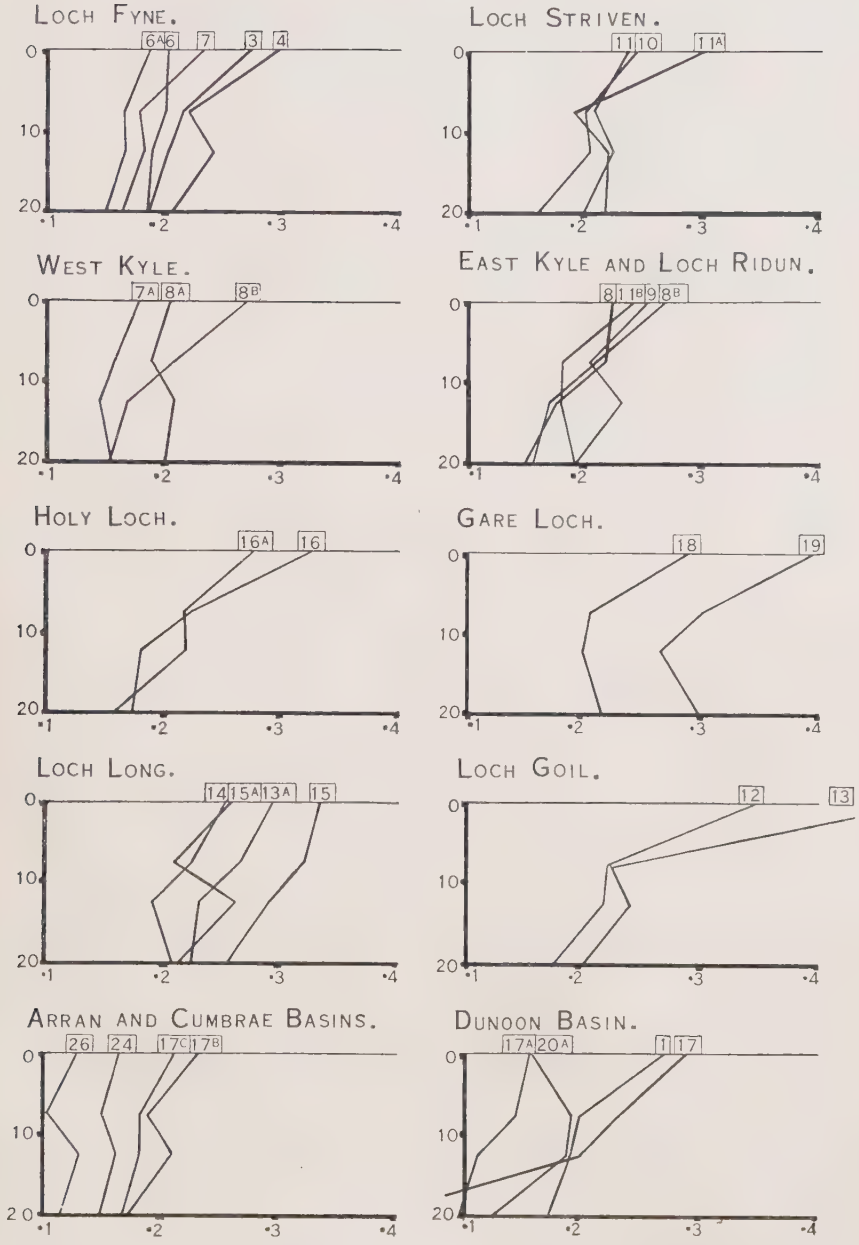

Fig. 3.—Distribution of phosphate with depth in the mud, in the main channels. Depth in cm. (ordinate) against % P_2O_5.

The most noticeable point, however, about the phosphate distribution, is the "Kink," or rise which so often occurs about the ten to fifteen-centimetre level in the mud. A kink, or change of slope of the curve, occurs in nineteen of the stations worked, and is so pronounced as to be an actual rise in thirteen of the stations : in some cases (St. 15a, 24, 26) it even rises higher than the surface values, which are usually far the highest. The significance of the kink is not known. The phosphate values themselves are high. While dropping low off shore, as at St. 26 by Ailsa Craig, they are lowest at sandy stations and those with a strong tide. Station 26, although showing a typical mud, and similar in appearance and texture to many found in the lochs, has a surface value for P_2O_5 of only 0·117%.

Where there is a heavy tidal action, the fine particles of the mud tend to be washed out ; also, the sediment in the water does not settle, and the phosphate value is correspondingly low. In these cases, the nitrogen value falls even lower, being in a more soluble form than the phosphate. This action of the tide is well shown in the case of Station 17a, which lies in 73 metres in a channel which shows typical mud at either end ; but in the centre of this channel, where for some reason the tide seems to be very strong, there is sand. The surface value here for phosphate is ·149 falling at the 15–20 cm. layer to 0·099, as against surface values of 0·267 and 0·244 for the stations above and below it in the same channel. The nitrogen values for these stations follow the same trend being, at the surface, 0·208, 0·069 and 0·188 respectively.

The phosphate values are highest in the Gare Loch and Lochs Long and Goil, the highest stations being 19, 15, and 13. The Gare Loch receives much rich silt from the river, which may account for the high values there. During the war there was sewage dumping at the mouth of Loch Long, but this would hardly affect the loch head. The cause is more likely to be found in the large streams entering these lochs, and this is born out by the high values found at Stations 16 and 16a in the Holy Loch, and 3 and 4 in Loch Fyne, both of which lochs are fed by large streams.

The distribution of the nitrogen in the muds is more erratic. Its variation with depth in the mud at the various stations is shown in Figure 4. The most outstanding point is the general fall of nitrogen value with increasing depth, which occurs in twenty-five stations, as against two with a rise, and six erratic. The fall in nitrogen with depth might be accounted for by a steady break-down of the organic nitrogenous compounds into nitrites and nitrates, and the removal of these by solution in the water.

Stations 18 and 19 are peculiar as regards nitrogen distribution, as they were for phosphates, and a type similar to them is found at St. 17,

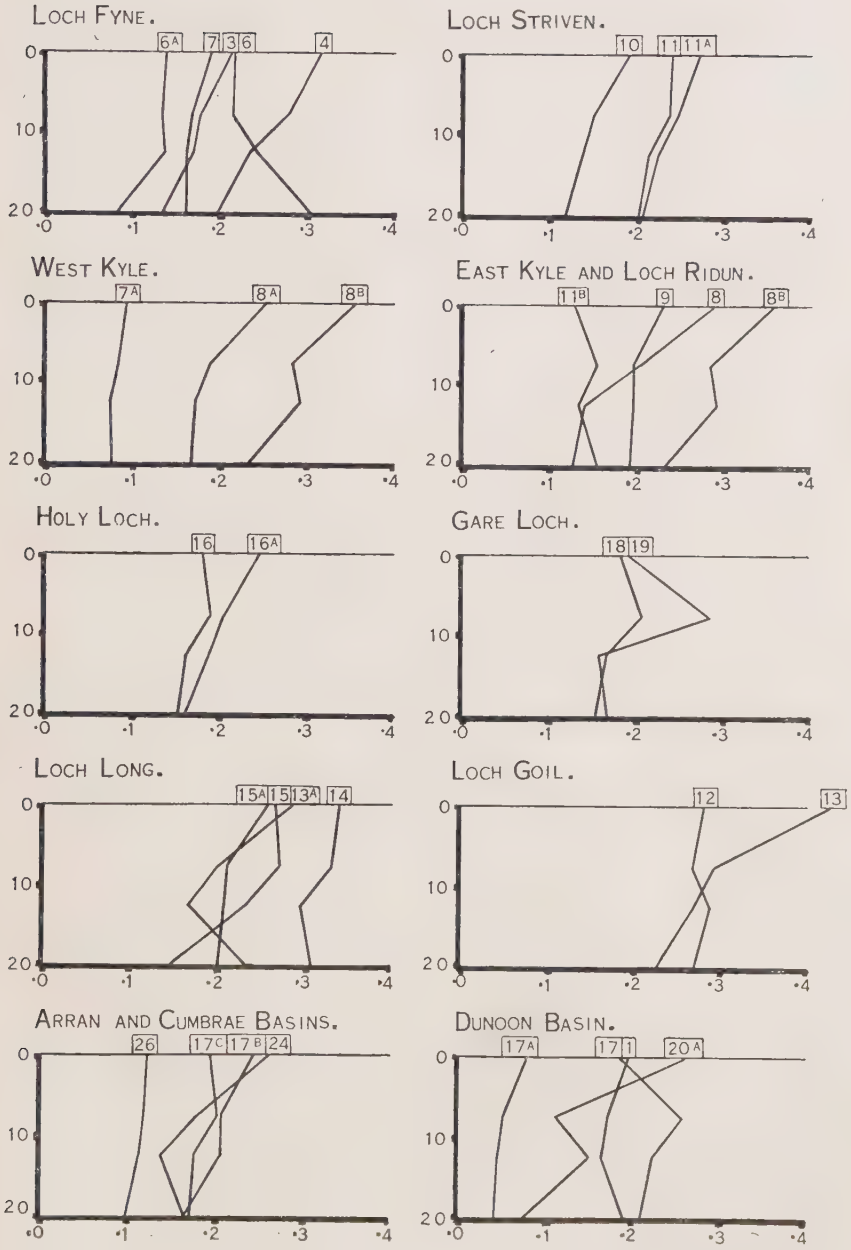

Fig. 4.—Distribution of nitrogen with depth in the mud, in the main channels. Depth in cm. (ordinate) against % N_2.

off Dunoon, where there is a fairly strong tide, though a typical mud. As is to be expected, the values are low in the sand at St. 17a, and in the sandy mud at St. 7a. They are very high at all depths at St. 14, and curiously they are also high at St. 8b where, though at the surface, at any rate, there is a strong tidal current, there is quite a typical mud.

Phosphate Nitrogen Ratio.

The ratio P_2O_5/N_2 also yields some interesting figures. There does not seem to be any constant relation of this ratio either to depth of water or depth in the mud, but in a chain of stations down any loch the ratio frequently varies similarly with depth in the mud, in successive stations. This variation, however, differs from one loch to another. Thus in Loch Long, the ratio tends to rise at first, and then fall again :—

	Depth in Mud.	Stations. 15	13a	15a
P_2O_5/N_2	0–5 cm.	1·22	1·10	1·00
	5–10 ,,	1·19	1·34	1·01
	10–15 ,,	1·21	1·38	1·26
	15–20 ,,	1·54	1·07	1·12
	20–25 ,,	1·38	0·97	—
	25–30 ,,	1·34	0·95	—

In Loch Striven, except the station at the loch head, the ratio tends to fall at first, and then to rise again

	Depth in Mud.	Stations. 10	11	11a	11b
P_2O_5/N_2	0–5 cm.	1·28	0·95	1·02	1·60
	5–10 ,,	1·34	0·87	0·77	1·16
	10–15 ,,	1·48	1·04	0·98	1·34
	15–20 ,,	1·38	0·99	1·02	1·27
	20–25 ,,	—	—	—	1·48
	25–30 ,,	—	—	—	1·54

The ratio is very high in the sandy Stations 7a and 17a, and also at St. 19 in the mouth of the Gare Loch, all of which stations have strong tides. It is lowest at St. 8b at the head of the Kyles, and then at St. 3 at Loch Fyne head, St. 12 at Loch Goil head, and St. 14 at Loch Long head.

Depth in Mud.	Stations. 7a	17a	19	8b	3	12	14
0–5 cm.	1·90	2·15	1·65	0·74	1·18	1·10	1·72
5–10 ,,	1·88	2·82	1·04	0·72	1·01	0·83	1·68
10–15 ,,	1·92	2·51	1·67	0·58	0·85	0·75	0·65
15–20 ,,	2·03	2·40	1·74	0·63	0·66	0·68	0·66

Figure 5 shows the nitrogen values in the 15–20 cm. layer, plotted against the corresponding P_2O_5 values. While, as is usual, the points are rather more scattered in the upper layers, with increase in depth they come more into line, and at this depth all but seven lie close to a straight line, as indicated by the two parallel lines in the figure. Certain stations lie outside these lines, and are discussed below. In the higher

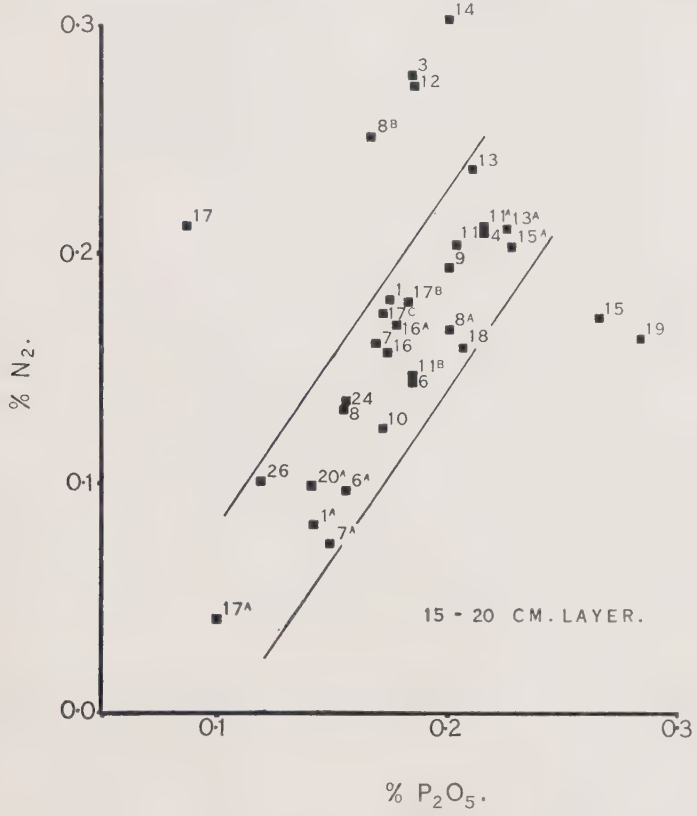

FIG. 5.—Percentage P_2O_5 against percentage N_2 in the 15–20 cm. layer throughout the area.

layers other stations also outlie, but come into line lower down. The extreme stations, too, are well in line, from the very low values in St. 17a, to the high values in the upper layers of Stations 13a, 15a and 19. The only stations which lie below the line in this figure are St. 15 in Loch Long, and St. 19 in the Gare Loch. In the layer five cm. higher, however, Stations 13a and 15a, both in Loch Long, also fall below the line, as well as St. 19. Stations 3, 12 and 14, which lie above the line, are all loch-head stations, near the entry of a large stream, and St. 8b and 17, which also

lie above, both have strong tides, though still remaining fairly normal muds.

Although subject to local irregularities, the successive stations down the various deep channels frequently conform to a typical pattern throughout the chain; and this type is distinctive for each chain. We have already shown that some of the lochs have typical ratio distribution curves. Similarly the curves for the distribution of phosphates, and nitrogen, are often closely linked in the successive stations of a chain, and frequently grade in character from the head to the mouth of the loch. This agreement within the chains, and the difference between the chains, is well seen as far as phosphates are concerned, in the following groups of stations (Fig. 3).

St. 10, 11, 11a, 11b. In Loch Striven.
St. 18, 19. In the Gare Loch.
St. 12, 13. In Loch Goil.
St. 17b, 17c, 24, 26. In the Cumbrae and Arran Basins.
St. 14, 15, 13a, 15a. In Loch Long.

In the case of the last chain, it is interesting to note that the curves for the upper three stations of the loch have an unusual form, similar in them all, whilst the lowest station in the loch (15a) has attained the more normal type, with a pronounced kink. In this it comes more into series with Stations 12 and 13 in the adjoining Loch Goil, which, though abnormal, shows a distinct kink. Whilst the Loch Goil chain and the upper part of the Loch Long chain show an increase of phosphate towards the mouth, the chain which runs out to Ailsa Craig shows a marked fall seawards.

The nitrogren distribution shows a similar behaviour in some of the lochs (Fig. 4) though often masked by local irregularities. Thus the Gare Loch, Loch Goil and the Holy Loch all show typical curves throughout. Here again the seawards stations, 24 and 26, show a decided drop in nitrogen values.

Finally I wish to express my thanks to the members of the staff of the Millport Laboratory, who have assisted throughout the work.

SUMMARY.

1. The P_2O_5 and N_2 contents of the muds at 33 stations in the Clyde Sea Area, have been determined, at 5-cm. stages, down to 20, and sometimes 30 cm. below the mud surface.

2. In estimating, the phospho-molybdic method for phosphates, and the Kjeldahl method for total nitrogen, were used.

3. There is no general relation between P_2O_5 or N_2 values and the depth of water, with the following exception :—

4. The P_2O_5 values in depths of less than 40 metres all lie close together.

5. The P_2O_5 values fall off with increasing depth in the mud, but usually show a rise at the ten- to fifteen-centimetre level.

6. The nitrogen values usually fall with increasing depth in the mud.

7. Stations with strong tides, usually have low P_2O_5 and N_2 values.

8. A chain of stations down a deep channel holds more or less to the same type of distribution curve throughout ; but the type of curve varies in the different chains and is distinctive of each.

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Salinity Interchange between Sea-Water in Sand and Overflowing Fresh-Water at Low Tide.

By

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With 1 Figure in the Text.

The following investigations were carried out in order to test the validity of the oft-recurring statement to the effect that "burrowing organisms live under fresh-water conditions during low tide in estuaries." This type of statement is usually made in respect to organisms which live in the sand or mud of estuaries in which, at low tide, a stream of fresh water passes over the ground in which the organisms are buried.

I have not been able to find any references to show that work has ever been done on this subject with the idea of determining the actual salinity of the water held by such sand. Therefore I carried out the following experiments to try to find if data could be procured which would be sufficiently consistent to lead to any conclusions.

Locality.

For preliminary purposes the experiments were carried out in a bay known as Traigh Allt Chailgeag on the North Coast of Scotland about three miles east of the village of Durness. Traigh Allt Chailgeag seemed very suitable for these experiments because,

1. The distance from H.W.M. to L.W.M. is short (250 yards),
2. At low tide a stream of fresh water flows across the sand,
3. The sand-grains are of fairly even size and the texture of the whole ground is uniform,
4. The animal population of the sand is small, since the bay is open to the north and is exposed to continuous heavy surf,
5. The slope is gentle and uniform,
6. There is a good depth of sand.

Apparatus.

The apparatus consisted of a number of glass tubes, each of 15 c.c. capacity, fitted with rubber stoppers; and a long glass pipette marked

off in inches and fitted with a rubber bulb of about 100 c.c. capacity. For use in sand of even texture the glass of this pipette need only be 5 mm. in internal diameter and 1 mm. in wall thickness. Further, it should be of uniform bore without constrictions or swellings.

Procedure.

Observations were made at a number of stations at measured distances along the course of the stream from H.W.M. to L.W.M. following the retreating tide. At each station samples were taken of 1, the flowing water of the stream, and 2, 3 and 4, the water in the sand at a depth of 2, 4 and 6 inches respectively.

The taking of the first sample from each station presented no difficulties. Samples 2, 3 and 4, which were from the sand beneath the flowing water, were procured by compressing the bulb and pushing the graduated end of the pipette into the sand to the required distance. The bulb was then allowed to expand slowly so that a quantity of sand and water was drawn up the tube. If the pipette be withdrawn and held vertically the sand will collect towards the open end, whence it can be ejected and the superincumbent water poured into a collecting tube and labelled.

At each station, before taking the samples, the depth and surface speed of the flowing water were measured. The speed was estimated by floating a thin slab of cork, 6 in. $\times$ 5 in. in area, on the surface of the water and measuring with a stop-watch the time taken to cover a known distance.

The depth of the water over the sand was measured with a thin glass ruler placed so that one of its edges was against the flow of the water.

The temperature of the atmosphere and of the flowing water was then taken.

The results at first sight appear to be somewhat erratic, but allowance must be made for the difficulties in sampling, as it is impossible to avoid slight admixture of water from higher layers when taking samples of those below.

As was to be expected, the flowing water was found to increase steadily in salinity from H.W.M. to L.W.M., although the final salinity was much less than might have been anticipated.

From the curves (Fig. 1) showing the salinity of the water in the sand at different depths there appears to be a possibility of dividing the area between H.W.M. and L.W.M. into three well-defined sections as regards the water in the sand, viz. :—

1. A section from H.W.M. down shore for a distance of 90 yards in which the salinity increases with great rapidity.

Table of Readings.

Date—8.iv.29. Weather—Mild, Wet. Wind—O.

Height of High Tide, 8.iv.29 — 13·3 ft.

*Tidal Data.**

Max. Height of Spring Tides — 14·4 ft.

Height of Low Tide, 8.iv.29 — 0·8 ft.

Fall in level from H.W.S.T. to L.W., 8.iv.29 — 13·6 ft.

Average Tide Heights from 8.iii.29 to 8.iv.29 { High Tide, 13·2 ft. / Low Tide 2·7 ft.

Average Tidal Range — 10·5 ft.

	Locality.	Time of Sampling. Hours before L.W.	Flowing Water. Depth.	Speed.	Temp.	S°/₀₀	pH	2 ins. in sand S°/₀₀	pH	4 ins. in sand S°/₀₀	pH	6 ins. in sand S°/₀₀
1.	H.W.M. in stream, Traigh Allt Chailgeag	11.30 a.m. G.M.T. 1 hr. 41 m. before L.W.	300 mm.	1 ft. per sec.	10° C.	0·35	7·0	2·25		1·55	7·0	12·42
2.	50 yds. below H.W.M. (all measurements made along the stream)	11.45 a.m. 1 hr. 26 m. before L.W.	150 mm.	1 ft. per sec.	10·5°	0·28	7·0	5·91		1·23		13·78
3.	90 yds. below H.W.M.	Noon 1 hr. 11 m. before L.W.	375 mm.	2 ft. per sec.	11°	0·35	7·3	18·12		16·62		24·15
4.	150 yds. below H.W.M.	12.15 p.m. 56 minutes before L.W.	75 mm.	1·4 ft. per sec.	11·5°	1·8	7·4	16·4		17·45	7·75	24·9
5.	200 yds. below H.W.M.	12.30 p.m. 41 minutes before L.W.	450 mm.	0·25 ft. per sec.	12°	5·43	7·4	29·47	7·75	29·47		29·02
6.	250 yds. below H.W.M. and just above L.W.M.	12.45 p.m. 26 minutes before L.W.	150 mm.	2 ft. per sec.	11°	8·08	7·5	32·57		34·34	7·85	

* Admiralty Tide Tables, Parts I and II.

2. A middle section of about 60 yards in which there is very little increase in salinity.
3. A final section of about 100 yards extending to L.W.M. in which the rate of increase of the salinity is comparable to that of the first section.

This would seem to indicate that towards H.W.M. and L.W.M. the salinity of the water, at least in the shallower layers of the sand, is subject to a certain amount of fluctuation with the tides, whereas in the middle portion there exists a condition of greater stability which may be explained in the following way. In each of the three sections a different set of conditions prevail. Section 1 is under fresh water for the greater portion of 12 hours ; Section 3 is under sea-water for the greater portion of 12 hours, while Section 2 is under fresh and sea-water alternately for approximately equal periods. Also, during neap tides Section 1 is never under sea-water, Section 3 is always under sea-water, but Section 2 is subject to both sea- and fresh water.

At most, however, the exchange in salinity between the overflowing water and the water in the sand must be extremely slow. For instance, although these readings were taken within a short period of a spring tide the salinity of the water in the sand at H.W.M. and L.W.M. at 6-inch depth was considerably different from that of the overlying water. The two areas over which the graphs are drawn is an attempt to express this in another way. Assuming that the slope of the beach is a straight line between high- and low-water mark, the time that any point between H.W.M. and L.W.M. is under fresh water or sea-water can be found approximately by comparing the relative lengths into which a vertical from that point is cut by the harmonic curve.* For example, if it be desired to determine the time during which a point 180 yards below H.W.M. is under fresh water, it is only necessary to take the vertical AXB. Then the proportions of sea and fresh water will be (since total time is AXB) $\frac{AX}{AXB}$ and $\frac{XB}{AXB}$ or $\frac{210}{300}$ and $\frac{90}{300}$ (hours) respectively of the time between H.W. and L.W. of that tide.

Depth and Speed of Flowing Water.

The relation between these and the salinity of the water in the sand does not appear to be very clear. Certain factors, not met with in the case

* This simple harmonic curve was drawn in accordance with the formula $h = \pm \frac{1}{2} r \cos \theta$ where h = height of tide above mean tide level.
r = range of tide.
θ is an angle $= \frac{\text{Interval from H. or L.W.}}{\text{Duration of rise or fall}} \times 180°$.

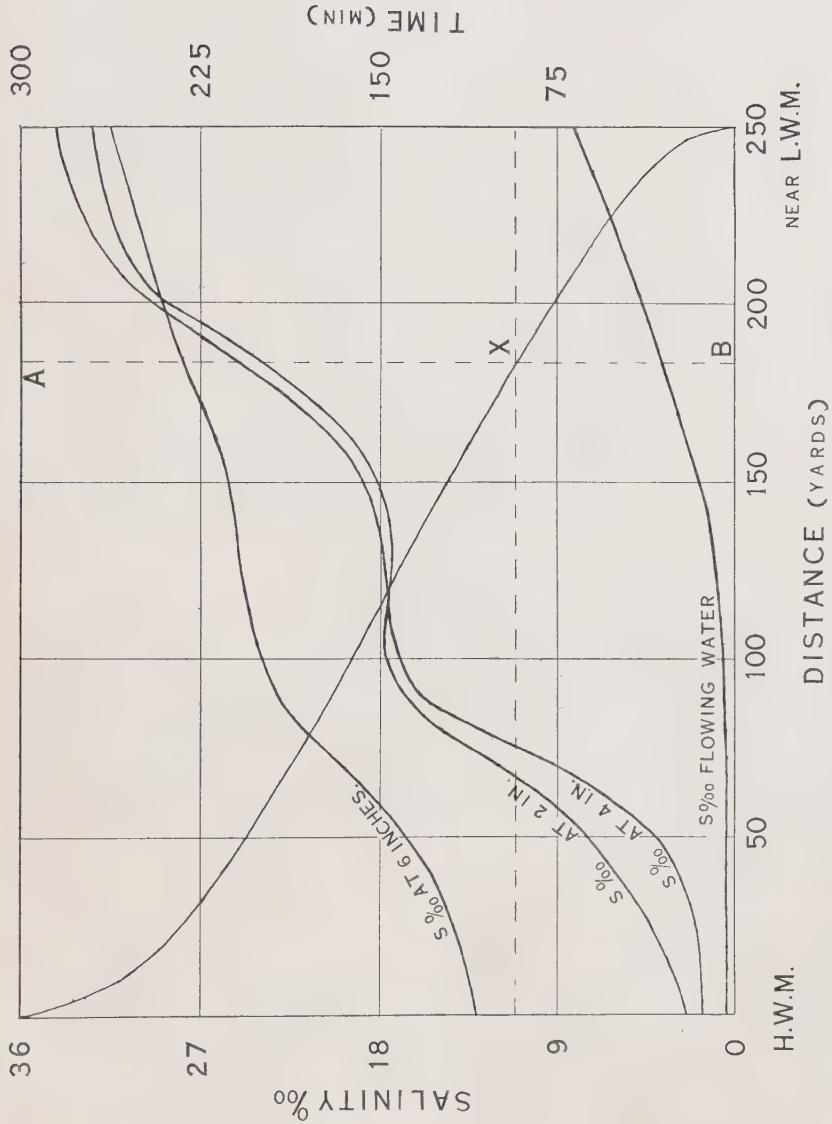

FIG. 1.—Curves representing the salinity of the water at various depths. These curves refer only to the times stated, they are not given as representing static nor minimum values.

of streams which flow over a more coherent bed, also appear to disturb the relationship between depth and speed. When a stream of fresh water flows over loose sand of even texture ripple-marks are rapidly formed. These impede the progress of the water so that, in the first instance, although the surface layers may be travelling at a fair pace, eddy formation may cause other degrees of speed or direction of flow in the other layers. The second stage occurs when the ripple-marks form a bar great enough to force the stream to change its course. This change of course take place with great frequency. In the deeper pools, also, certain peculiarities are noticeable. The walls are much more vertical than might be expected, so that the through flow is limited to the surface layer while the rest of the water eddies slowly round. In these experiments no apparatus was available for estimating the speed of any but the surface water.

From this it will be seen that there are a great many small factors which play a part in determining the speed and volume of the flowing water and its effect on the salinity of the water in the sand. Some of these factors would appear to balance others, so that, for the present at least, it might be advisable to disregard variations in speed and depth, and, by taking an average, consider them as constant (speed = 1·2 feet per sec., depth = 250 mm.).

CONCLUSION.

In conclusion, it would seem that a stream of fresh water passing over inter-tidal sand has little effect on the salinity of the water in that sand to any great depth. In all probability, at a depth of 10 inches (although, doubtless, grading down slightly towards H.W.M.) the salinity will be similar to that of the sea. Organisms, therefore, which burrow in the sand may easily remain under tolerably constant (salinity) conditions no matter what be the state of the tide.

Studies on Conditioned Responses in Fishes. Part II.

By

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With 11 Figures in the Text.

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I. Introduction.

The present paper continues the account of my experiments on the capacity of fishes to form conditioned responses towards definite stimuli under strict experimental control. No change has been made in the method of recording the results except in the section on auditory discrimination in the wrasse. This slight variation is explained in the appropriate place.

All the experiments described in this part belong to Section A of the previous paper (**1**), in which food is the unconditioned stimulus. The work which has been carried out in Section B will receive fuller treatment at a later date.

II. The Capacity of the Wrasse, *Crenilabrus melops* (L.), to Differentiate between Two Different Sounds.

Being a continuation of the experiment described in Part I, p. 508.

Mention was made in the earlier paper (**1**) of the likely continuance of discrimination experiments with a wrasse which had already formed a stable conditioned response towards the stimulus of a tuning-fork vibrating at the rate of 128 d.v.'s per second. The discrimination attempted was a simple one, in which the fish had to establish an association between two new factors, in the form of an electric buzzer and a food-bottle at one end of the tank, as distinct from the original response involving entry to a food-bottle at the opposite end of the tank. In Figure 8, Part I, of these studies (**1**), page 508, B1 represents the position of the new food-bottle and its associated buzzer. All other parts are unchanged. The buzzer was of a common type used as a door-bell, enclosed in a stout brass box with a thin brass diaphragm, giving a somewhat harsh note of high pitch approximating to the note F in the 2nd octave of the pianoforte scale, contrasting very strongly with the rich low note from the tuning-fork.

The results are given in Figure 1, a diagram requiring more detailed explanation for the sake of clearness. In any one section of this there is firstly a continuous base line along which dates are marked off as before. Above this are three horizontal sets of positions, the median one shown as a continuous dotted line. Where the original tuning-fork was used as the conditioning stimulus that test is denoted by the symbol O, the symbol X signifying the uses of the buzzer as the signal. Each such symbol O or X entered at regular intervals along the record represents a single test, and the position of it in relation to the dotted line gives the behaviour of the fish.

Thus, referring to the first day's work recorded in the diagram, November 29th, it is to be seen that 7 presentations of the auditory stimulus were given that day. The first two of these being the buzzer, X. the next two, the primary stimulus of the tuning-fork, O. If the fish entered food-bottle B (the original response), no matter which stimulus preceded it, the diagram records a line starting from the median dotted line, then directed upwards to the symbol, and back again to the dotted line. Such, for example, was the response to the buzzer at the first of the tests recorded. If entry was to the opposite bottle B1 (the new response), there is shown a similar line directed downwards, and back again. At the fifth test of the first day this is the result recorded, the correct one for that stimulus—the buzzer. Should a vacillating response be the result, the fish going first to one bottle and then to the other, the order and course of this is shown as in the sixth test of the first day,

by a dotted line in the corresponding directions, the symbol occurring at the top or the bottom depending on whether it was bottle B, or B1, in which the fish finally came to rest. In the sixth test just mentioned, this was B1, the correct one. Not infrequently, there was no decisive entry to either bottle, and this is shown in the record by the appropriate symbol remaining on the dotted middle line, as, for example, in the last test of the day.

With this explanation the diagram becomes a concise picture of the

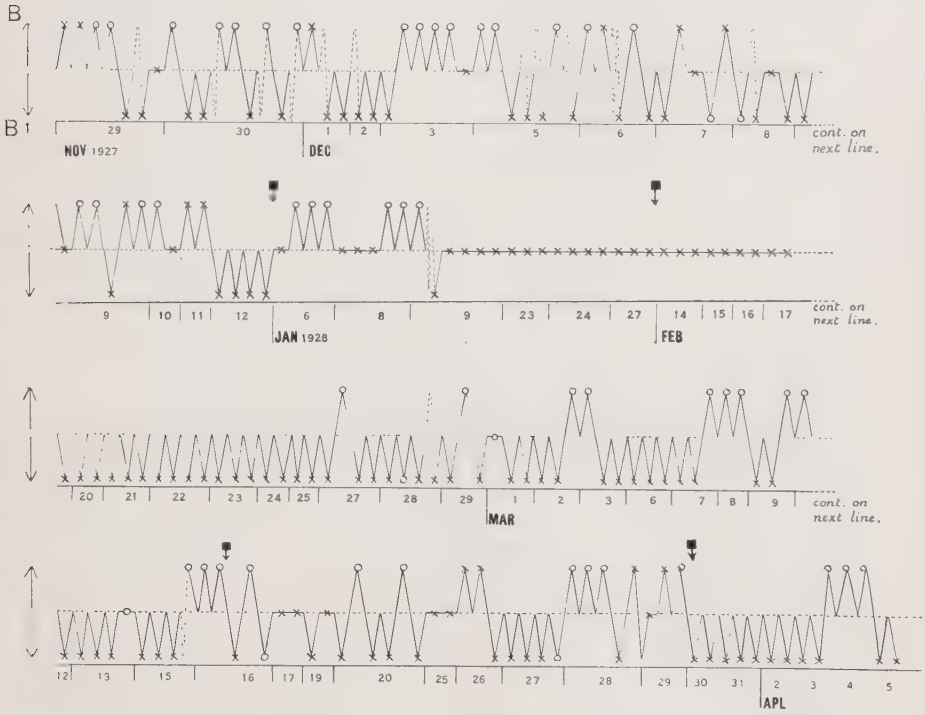

FIG. 1. Record of the discrimination between the sound of a tuning-fork and the sound of an electric buzzer shown by the wrasse, *Crenilabrus melops*, in the formation of conditioned responses.

Explanation in text: O = tuning-fork; X = buzzer.

results obtained, but the more salient points may be outlined in a running commentary.

The introduction of the second bottle and the buzzer at once interfered with the very clear-cut result of the earlier experiments. Although on the first two occasions when the buzzer was used as the signalling stimulus the actual swimming response was a wrong one from the conditioned response point of view, yet the fish, in order to obtain the food used at those tests, finally entered the new bottle. Watched for

some time between these and the next tests, the fish was seen to go first to the old bottle and then into the new one, showing an obvious and rapid learning of the relationship of the new bottle to food. It was a striking feature of the earlier conditioned response to the tuning-fork stimulus, that after entry into the food-bottle the fish continued to remain there making signs fairly to be described as anticipatory, until such time as food was given, if the giving of food was intentionally delayed, or not given at all; with the greater complexity this behaviour was somewhat modified. After entry into the food-bottle, the fish usually stayed but a short time, a few seconds, then swam away, to return after a greater or lesser interval.

Examination of the record up to the break denoted by the first arrow reveals the following interesting points in the response. Statistically, there is an indication that the fish correctly associated the buzzer, and the tuning-fork, with their respective food-bottles. But it is to be seen that the response bears some relationship to the previous, immediately preceding response in many of the tests. Thus, at the fourth test of November 30th, there is shown that the fish went first to bottle B1, and then to B, the correct one for the stimulus, for, at the previous test, bottle B1 was used in conjunction with the buzzer, and the response was correctly given. A similar effect is seen at later tests on the same date, as also on December 5th, 6th, etc.

On December 12th, shown by the first arrow, experiments were temporarily suspended. From the commencement of the differentiation tests, until this date, the general result had been inconclusive, with some evidence that instead of discriminating more easily, the fish was becoming more confused. From December 7th to 12th the number of incorrect responses had decidedly increased.

The break which now occurred was of 24 days' duration, and lasted till January 5th, 1928. During this time, the fish was fed for me by Dr. Amirthalingam, to whom I owe my grateful thanks.

One very obvious fact emerges from a study of the responses given immediately after this date. It is to be seen that where the buzzer was used as stimulus, no definite response was noted, the fish not entering either bottle during two minutes' observation at these tests; whilst, on the other hand, when the tuning-fork was sounded, it at once elicited the original response of entry into bottle B. The explanation of this is probably to be found in the fact that this last is a much older, and therefore more stable response, for all my previous work shows that these responses, when once thoroughly established, are stable over long periods. The response involving entry to B1, associated with the buzzer, could not as yet be regarded as well established, and further, many incorrect responses had previously resulted when the buzzer was used. It was

therefore decided, on January 27th (2nd arrow, Fig. 1), to continue with the buzzer alone, in the hope of establishing the response when not complicated by intermittent presentations of the sound of the tuning-fork. But for a while the fish ignored all food, and it was not until February 14th that a serious start could again be made. At the next 9 trials, up to February 17th, there were still no signs that the process of forming this association was in any way advancing, so that it was somewhat surprising to get a clear-cut response to B1 at the third test of that date. This, however, initiated a fairly lengthy period from February 20th to March 15th, during which, at 45 separate trials, the fish never failed to enter bottle B1 when the buzzer was used as conditioning stimulus ; 15 presentations of the tuning-fork were given at irregular intervals from February 27th, the original and correct response resulting at twelve of these, and an incorrect one at only one test. On the remaining two occasions no response occurred, nor was food eaten when given. It appeared then that, by this date, the fish had truly learnt to discriminate between the sound of the buzzer, and that of the tuning-fork. There still remained the possibility, however, that it was the relative positions of the two sounds which was being discriminated, and not the sounds themselves. This was put to the test by placing the buzzer over by the bottle B at the opposite end of the tank, but otherwise continuing the tests unchanged (3rd arrow, March 16th, Fig. 1). During the next two weeks thirty tests were made. Of these, twelve tests gave a correct response to the buzzer, but ten were incorrect ; two out of seven presentations of the tuning-fork were also followed by the wrong response. Here was a clear indication that it was the *position* of the two sounds which had been the factor discriminated. So on March 30th (4th arrow, Fig. 1) the buzzer was replaced in its original position. When tests were resumed there was no hesitation such as had persisted before this change back. The responses towards both the buzzer, and the tuning-fork, were given rapidly and correctly until April 5th, when the experiment was concluded owing to my taking up duties elsewhere.

There is ample evidence in these results for the conclusion that *this specimen of a common wrasse,* Crenilabrus melops, *could rapidly form a stable conditioned motor response involving entry into a special bottle for food, using as the conditioning stimulus either a tuning-fork sounding the note lower C, or an electric buzzer giving a mixed note corresponding approximately to the note F in the 2nd octave, when these were used singly.*

It could not, however, differentiate between these two sounds as sounds, if they were used to build up a differential response. The factor discriminated in such tests was found to be the place of origin of the sound, not the quality or nature of the sound. In this respect, the auditory sense of this fish appears to resemble the visual sense, when investigated in the same

manner, for in reviewing the evidence on pp. 516 and 519 of the earlier paper (**1**) the conclusion was reached that in visual differentiation the *source of light* played a greater part in the discrimination than a wide range in the *intensity* of the two lights. Finally, it is interesting to note how strongly these conclusions upon two senses of major importance to man and most higher vertebrates contrast with the conclusions already reached upon the fineness of perception shown by the blennies in forming these responses towards thermal and salinity changes, and towards gustatory stimuli, such as are described in a later portion of the present paper.

III. (*a*). The Capacity of the Plaice, *Pleuronectes platessa* (L.), to form a Conditioned Response towards *Visual* Stimuli.

The experiments described in this section, including the present one and the two following, were carried out in order to ascertain whether the

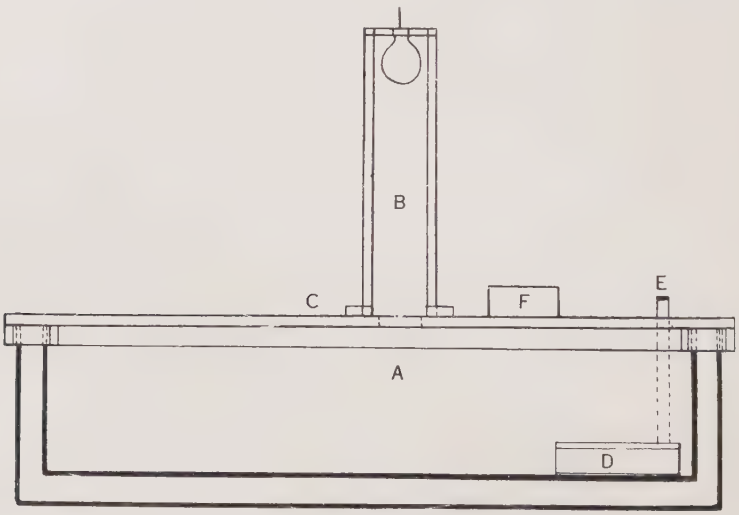

Fig. 2.—Diagram of apparatus used in the formation of a conditioned response in the plaice towards *visual* stimuli. Description in text.

results previously obtained with the wrasses (**1**, p. 510) were to be obtained generally amongst fishes of different habits.

Essentially, both the apparatus and the mode of experimentation were the same as there described, but minor changes were made to suit the conditions at the Cullercoats laboratory, where they were carried out. Figure 2 is a diagram of the tank and general arrangement. The tank was of concrete, 2 ft. by 3 ft. 6 in. by 10 in. deep. It was completely covered in, to exclude all light. A small hole, A (Fig. 2), 2 in. square, was

cut out of the top, over which was placed the light chamber B, with a lantern slide-holder C at the lower end for use with Wratten light filters. The food-box D was rectangular, measuring 9 in. by 6 in. by 2 in. deep, with an opaque tube E leading down into it at the hindmost end, for the introduction of food. A periscope F fitted over the entrance to the food-box served to note the response.

The visual stimulus was the unscreened light of a 100w. opal gas-filled electric lamp, 12 in. from the water surface, suspended in the light chamber.

The mode of experimentation was at first the normal one for the type of experiment, i.e. light switched on, food in the form of a small piece of Mytilus introduced 30 seconds later; light then switched off after a further 30 seconds. But on December 8th, 1928, I was led to change this procedure in a marked manner. The reasons for this can be revealed in a

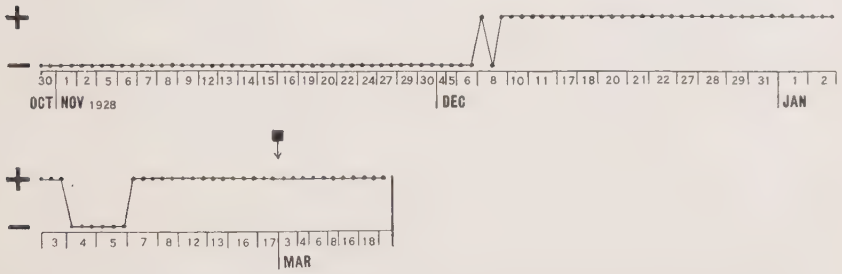

FIG. 3.—Record of the process of formation of a conditioned response in the plaice towards a *visual* stimulus. Explanation in text.

few words. It is to be seen from the diagrammatic record of the results in Figure 3 that the period of learning, or the period during which no positive conditioned response was noted, was a somewhat lengthy one (October 30th to December 8th). It appears from the record that the response came suddenly into operation on December 8th, and remained constant for a long period after. This early negative stage is therefore, I think, probably incorrectly recorded. I was puzzled at the unusual length of time which this fish was taking to build up the response, as compared with other fishes investigated. I had noticed also that, although a full 30 seconds was allowed after food was introduced, and before the light was switched off, the fish never became visible beneath the periscope during that time, yet on performing the next test, one hour or so later, the food had been taken. On December 8th, then, I removed the periscope, which only allowed of a limited field of vision, and settled down to watch the behaviour of the fish from the time the light appeared, taking especial care to remain quiet and still. As these tests were all

carried out in late evening, the room was always in darkness, and it was not difficult to remain unobserved. By this means I was able to discover that the behaviour of the plaice was strikingly different from that of any of the other fishes with which I had worked.

For one minute the fish made no movement whatever. It then commenced to move slowly and hesitantly towards the illuminated area at the opening of the food-box, but with a curious side-to-side movement—a short swim at an angle to the right of the direct path, then pause—then another short swim at an angle to the left—and in this erratic, slow, zigzag way the fish approached the opening of the food-box. Still with the same hesitant zigzag motion it entered completely into the food-box. After remaining motionless in the food-box for a further space of time, the fish suddenly took the food in the box, and then backed away quickly to a remote corner of the tank. The conditioned response was thus at this time already well formed, for the whole movement, though lasting twelve minutes, was directed in an obviously purposive manner. It should be added that, in the very early stages of conditioning, food was not introduced directly into the food-box only, but was divided into two portions, one of which was dropped into the tank at the opening of the food-box where it could be seen from any part of the tank, and the other placed in the food-box. It is clearly impossible to build up this response without doing this.

As a result of the observation just described, the light was left on in all subsequent tests for 15 minutes, or until such time as was required for the fish to complete the response, watching the whole time through the periscope. It soon became apparent that the suggestion that the response was already well-formed by December 8th was correct; for the behaviour of the fish at that test was typical of the conditioned response shown by this fish throughout the remainder of the tests. There was some variation in the time taken by the fish to enter the food-box completely, but it was rarely less than 2 minutes and more usually was 6 to 8 minutes. If no entry occurred within 15 minutes, as on January 4th and 5th, the response was regarded as negative. The fish ignored all food on these two days. With this exception the response was obtained at the whole of the tests made up to the date upon which the experiment was concluded, March 18th, 1929. This statement, however, ignores the fact that from January 18th to March 2nd the fish constantly refused all food, which was a feature shown by most of the aquarium fishes for the whole or portion of this time, owing to the intense cold then prevailing. An arrow indicates this date in the record. It was most interesting to find, when feeding was once more resumed on March 3rd, that the conditioned response had been in no way diminished in strength, or altered in nature by this long abstention. Such a high degree of retention, supported as it

is by many similar instances from my other experiments, lends additional support to a suggestion made by me recently (3) that associations of this nature, when set up in natural conditions, may acquire sufficient stability to bring about a permanent change in the habits of a large body of fish, through the purposive association (by one or more of these fish) of some slight change in an environmental factor with more advantageous conditions of living.

III. (*b*). The Capacity of the Coal-fish or Saithe, *Gadus virens* (L.), to form a Conditioned Response towards *Visual* Stimuli.

The apparatus and mode of experimentation was the same as that used in III (*a*).

The results are given as a diagrammatic record in Figure 4.

The fish used was a small male, 14·5 cm. long. The experiment was carried out alongside that on the plaice, using a similar 100w. opal gas-filled electric lamp as the conditioning stimulus. Eighteen associations

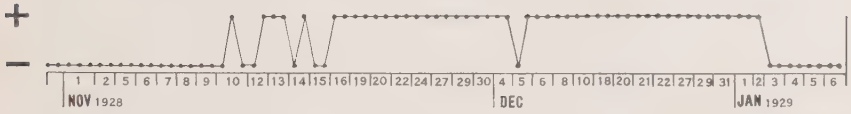

Fig. 4.—Record of the process of formation of a conditioned response in the coal-fish towards a *visual* stimulus. Explanation in text.

spread over the period October 31st to November 9th, 1928, were required before the first conditioned response was obtained. This was followed by a short period when the response was uncertain, lasting over a further period of nine trials of which four gave a positive response, and after November 16th the response was firmly established. On January 3rd the fish ceased feeding, and at tests carried out from the 3rd to the 6th January a completely negative result occurred. The fish was in a torpid condition. It may be recalled that the plaice also went off food on January 4th and 5th as well as from January 17th onwards. No further tests were made on the coal-fish after January 6th as it continued to refuse all food, and it eventually succumbed to the severe cold at the end of the month.

The diagrammatic record of the results needs no further comment.

The individual behaviour of this fish closely resembled that shown by the wrasses under these conditions. At an interval of from 10 to 25 seconds, no matter what was its position in the tank, the fish swam rapidly to the food-bottle, taking the food quickly when given, and swimming away again with equal rapidity.

III. (*c*). The Capacity of the Cod, *Gadus callarius* (L.), to form a Conditioned Response towards *Visual* Stimuli.

Essentially a repetition of the last experiment, the conditions of the test remaining unchanged.

The results are expressed in diagrammatic form in Figure 5 and require little comment, so closely do they follow those obtained in the last experiment. The commencement is shown as March 9th, 1929. Actually the experiment began on February 23rd, upon which date the fish was placed in the tank. Work was not at once possible, as the fish remained in a torpid state, eating no food, in common with the other specimens at this time. When more lively habits were shown, learning was fairly rapid, only nine days, covering 21 associations, being required before the first conditioned response was obtained. For a further period of 4 days, including twelve trials, the result was uncertain, but thereafter the

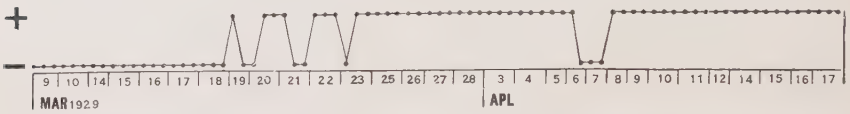

Fig. 5.—Record of the process of formation of a conditioned response in the cod towards a *visual* stimulus. Explanation in the text.

conditioned response was given invariably, except on April 6th and 7th, for which no reason was apparent. The experiment was concluded on April 17th. After my return from a cruise the fish was removed, and used for work on thermal stimuli to be described later.

IV. The Capacity of the Blennies, *Blennius pholis* (L.) and *Blennius gattorugine* Bloch, to form Conditioned Responses towards Gustatory and Olfactory Stimuli.

Blennies were again chosen to make the preliminary investigations into these two stimuli on account of the ease with which their responses can be noted and also for their general adaptability. They are additionally well suited to the object in view, since they are fishes which normally capture food by sight and not by taste or smell, so far as can be judged from ordinary observation. At the Plymouth Laboratory I used *Blennius gattorugine* throughout, but this species being rare at Cullercoats, it was necessary, on continuing the work there, to carry on with *Blennius pholis*. It is not, I think, likely that these two species should differ greatly in their response to this stimulus, but it is by no means improbable that there may be some slight variation, so the fact should be remembered in considering the results.

The Apparatus.

After many slight modifications the apparatus shown in Figure 6 was the one finally used. It differs but little from the apparatus used in the earlier experiments on blennies. The whole of the right-hand side of the figure is exactly the same as that of Figure 5, p. 503, of the earlier paper (**1**), whilst the remaining parts in the left-hand side of the figure are simple changes to meet the requirements of the present stimulus. A is a straight 10-in. Liebig's condenser from which the inner tube was removed, graduated, and then replaced, afterwards connecting it with the tube E

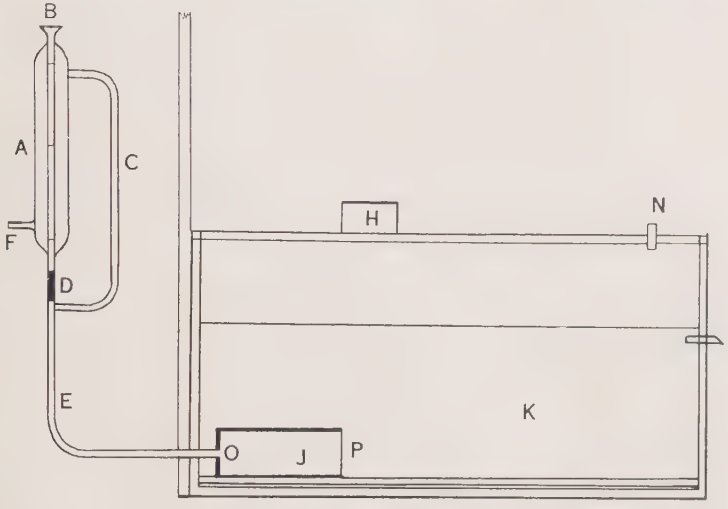

Fig. 6.—Diagram of apparatus used in the formation of conditioned responses in blennies towards *gustatory* and *olfactory* stimuli. Explanation in text.

which supplies the water to the aquarium *via* the home jar of the blenny. Water from the main aquarium supply enters the condenser at the lower end F, passes upwards in the condenser and down again through the tube C, to enter into the inner tube E, immediately below the pinch-cock D. The solution to which the fish is to be conditioned is placed in the inner tube at the funnel B. By this system absolute equality of temperature is assured. The pinch-cock D is of a type familiar to many chemists but possibly not to biologists. It is especially easy to use, and accurate and noiseless in delivery, so that it is far preferable to the ordinary patterns for this purpose. A description is given by Sutton (**2**). The rate of flow of the main current of water into the tank was maintained constant at 20 c.c. per second.

Method of Experimentation.

The routine of the tests was again that of the salinity and temperature experiments. The taste solution is placed in the inner condenser tube and left for ten minutes for temperature equalisation. When ready, pinch-cock D is opened and the experimental solution flows into the main stream; 10 c.c. was used and the time taken to enter the ingoing stream was 5 seconds. Food is dropped into the tank 15 seconds later through the opening in the screen N. The fish, if healthy, and desirous of food, at once swims to the spot, takes the food, and returns to its jar. The object in view, as in previous experiments of a similar nature, is to ascertain whether the fish can build up the response involved in the capture of food, to the stimulus of the solution serving as signal for that food.

The Results.

These are of two kinds—those obtained with the use of "natural" sapid solutions, and those resulting from the use of an "unnatural" or artificial substance in solution.

A. *Results obtained with "natural" substances.*

At the Plymouth Laboratory, nereid worms was the food most readily available. In all the experiments on *Blennius gattorugine* which were made there, the gustatory stimulus took the form of extracts of these worms, obtained by grinding up the worms with sand and sea-water, and afterwards filtering the resulting extract till clear, using the vacuum pump and glass-wool. At Cullercoats, Mytilus and Patella formed the main food supply. Extracts of these were made in the same way.

Specimen No. 1. *Blennius gattorugine*, ♂, 12 cm.

After being installed in the apparatus on August 14th, 1927, it was thought first of all, that it would be interesting to attempt to build up the conditioned response towards a solution which had merely stood in contact with the living worms in an intact and healthy condition. From August 15th to 31st such a solution was given three times daily unaccompanied by food but without any resultant response. The solution was made by taking several worms, and after washing them thoroughly in sea-water placing them in 100 c.c. of sea-water for 24 hours. It was soon felt, however, that there was little chance of stabilising the strength or nature of this solution, and the experiment was then dropped. On September 1st a fresh start was made with the definitive worm extract made in the manner described above, and in the first place, of a strength of 0·5%, i.e. 0·5 grm. of *Nereis diversicolor* (live, wet weight) to 100 c.c. sea-water.

A diagrammatic record of the results is given in Figure 7.

After no more than nine associations of this solution, the conditioned response became apparent at the first test made on September 3rd. Two further tests on the same day gave no observable response, but the fourth again produced it, and from then onwards it became firmly fixed. The generalisation of stimuli observed with others was again found to occur here, for two days later, on September 5th, when a 0·1% solution, indicated in the diagram of the results by a well-defined square dot, was tried, three successive tests elicited the conditioned response. Three succeeding tests with the original 0·5% extract diluted ten times, i.e. a 0·05% solution (shown in Fig. 7 by black triangle) were followed at the first by no observable response, but at the two following ones by well-marked positive responses.

It should here be added, that in order to eliminate any possibility that

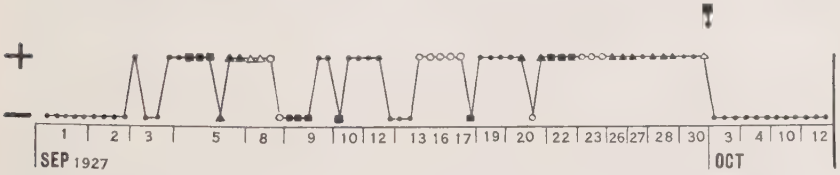

Fig. 7.—Record of the process of formation of a conditioned response in *Blennius gattorugine* towards gustatory stimuli. *Specimen* 1. Explanation in text.

●=0·5% extract of *Nereis diversicolor* (primary stimulus).
■=0·1% ,, ,, ,,
▲=0·05% ,, ,, ,,
o=0·02% ,, ,, ,,
△=0·01% ,, ,, ,,

some movement or change in conditions other than that of the worm extract might be responsible for bringing about the response, frequent controls were carried out. On September 8th, 12th, 20th, 22nd, and 29th, all possible movements of taps and tubes were made several times over, but using the aquarium sea-water only in place of the worm solution. Not one of these was followed by an observable response, and it can be safely asserted that this solution was indeed acting as sole stimulus. After the control tests had been made on September 8th, the fish was presented with a solution only one-fiftieth the strength of the original or primary stimulus, i.e. a 0·01% solution (shown in Fig. 7 by an open triangle), and the conditioned motor response again occurred at two such tests. A little later in the same day a 0·02% solution (shown in Fig. 7 by a plain circle o) brought about the response, but several hours later this failed to do so. The following morning, September 9th, tests one to three, this negative result continued with the 0·01% solution, but later in the afternoon, when presented with an extract of the original strength, 0·5%, the fish gave the characteristic response.

A study of the diagrammatic record up to the date indicated by the arrow shows plainly that the response was being given with greater certainty, as the number of associations was increasing, negative responses being given only on isolated occasions. It is noteworthy also that the conditioned responses could be brought about with any of the solutions tried, i.e. solutions containing from 0·01 to 0·5% of worm. This experiment thus provided the first indications obtained by me, that this type of stimulus may be as generalised in its perception by the fish, as the thermal or salinity changes previously recorded. I had hoped to begin a complete investigation into the extent of this, but on September 30th (arrow) I found that the fish had inexplicably got out of the tank and was picked up from the floor almost dead. It did, in fact, recover sufficiently to give the appearance of normal health and tests were carried out with the primary stimulus, 0·5% solution, up till October 12th, though quite without any signs of obtaining the conditioned response ; neither would the fish take food. On the 12th it was found dead. The figure shows plainly the inhibitory effect of such a disturbing influence.

In considering the results, and their bearing on the actual perception of the stimulus, there is a further factor to be considered. Whilst being introduced into the main stream of water entering the tank, the gustatory solution is subjected to dilution. Measurements of time of flow, and the quantity of water passing in that time, show that this dilution is approximately ten times. On account of diffusion this would be still greater when it reached the receptors of the fish.

With this fish then, it was shown that, not only was it able to perceive, but it could also form a conditioned response towards, a solution containing 0·5 grm. of worm in 100 c.c. of sea-water, and that it could react similarly towards one containing 0·01 grm., and to various intermediate concentrations.

Specimen No. 2. *Blennius gattorugine*, ♀, length 13 cm.

After being used for experiments described in the next section, this specimen was taken to repeat the observations made on Specimen 1. Work was begun at once, as the fish had already been in the apparatus the whole of the previous month. The stimulus was the same as the primary one in the last example.

The results are presented in Figure 8. The general impression received is that the results are not of the clear-cut and decisive nature which it is so desirable to obtain, in order to arrive at any positive conclusions upon the sense of discrimination. So erratic was the behaviour of this fish that this stage was never reached, yet the results are none the less interesting from other points of view when examined. In the early stages, after the second day, the actual behaviour of the fish showed

clearly that the stimulus was being perceived. When the sapid solution was entering, the fish frequently made irregular body movements, accompanied by the peculiar gulping and chewing movements of the mouth, such as were noticed in the advanced stages of the experiments on blennies with thermal and other stimuli. In the description of these, I referred to these movements as additional features of the conditioned response, occurring only when this was firmly established, and to be regarded as anticipatory in nature. These movements are such as might be actually expected if the stimulus was affecting the taste buds of the mouth region. But there is also some individuality about it, for it was not seen at any time in specimen 1, and in all the experiments where it has appeared, it has only done so after one or more associations of stimulus with food. Beyond this, there is nothing in the diagrammatic record which needs further comment.

It is a fitting place, however, to make a few general remarks upon the

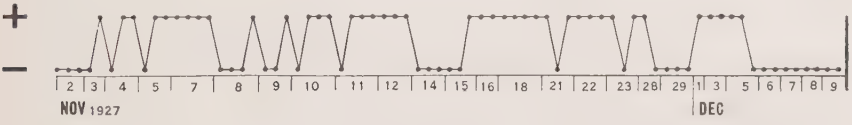

Fig. 8.—Record of the process of formation of a conditioned response in *Blennius gattorugine* towards *gustatory* stimuli. *Specimen* 2. Explanation in text.

use of this method in investigating any total behaviour response. If such a record as that showing the results of the present experiment were the result of an ordinary subjective type of experiment with a similar object, it could not be regarded as satisfactory positive evidence of gustatory perception. Such a result in those circumstances would need to be analysed statistically, and in considering the whole period of the experiment, it would be found that there are 40 occasions where the conditioned response was evoked, 33 where it was not. It would be concluded that the evidence is indeed slightly in favour of a positive perception, but nothing more could be said. On the other hand, under the conditions of the present tests, and by very reason of the nature of the response studied, it is not permissible to use a mathematical analysis of the record to determine whether *chance* has, or has not, played any part in the result after the response has once been built up. The *real* reason for the irregularity of the conditioned response in this fish must be sought in some internal factors of the fish, which are unknown to us. It was, for instance, from the moment when it was brought to the Laboratory, of a sluggish nature. On December 9th the experiment was stopped whilst I was absent from the Laboratory until January 5th, 1928. During this time the fish was plentifully supplied with food, but none

was eaten ; more significant still, the abdomen was found distended with eggs when I returned. It was therefore impossible to continue the experiment further as previous experience had shown what has since been abundantly confirmed, that the onset of gonad development in female fishes entirely inhibits the building up of conditioned responses. I have no evidence that it does so in male fishes.

Specimen No. 3. *Blennius gattorugine*, ♂, 11 cm.

The taste experiments in this example were again preceded by other experiments described in the next section which lasted from January 26th to February 27th, 1928.

The results are presented in Figure 9, showing a typical picture of conditioned response formations in fishes. From February 28th to March 27th (arrow) the fish was given 38 associations of a solution

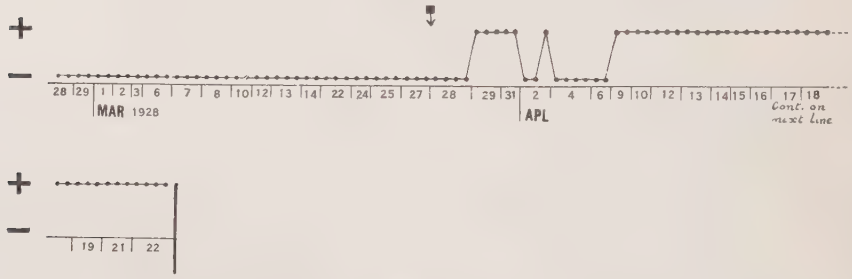

Fig. 9.—Record of the process of formation of a conditioned response in *Blennius gattorugine* towards *gustatory* stimuli. *Specimen* 3. Explanation in text.

containing 1 grm. of worm in 1000 c.c. of sea-water, i.e. a 0·1% solution, but no signs of the conditioned response appeared. It was therefore decided on March 27th to increase the strength of the extract to 0·4%. With this new solution four further associations only were required to bring about the conditioned response, accompanied also by vigorous mouth movements which had not appeared with the lower concentration. After a short period of no responses, from April 2nd to 6th, the responses became definite and never failed to appear at the remaining associations made until the experiment was concluded by my leaving Plymouth for Cawsand.

Specimen No. 4. *Blennius pholis*, ♀, 11 cm.

Results in Figure 10.

After being used for experiments in the next section, it was found impossible to continue at once with the experiments with sapid substances, owing to the development of the ovaries, and the refusal of food. These eggs were shed in March, 1929. The fish was again feeding freely by

April 2nd and a start was made on April 3rd (shown by arrow). The portion of the record preceding this represents the results with artificial musk as stimulus, which are here included in the same figure, in order to contrast a consistently negative result with the typical result obtained when perception is positive.

The conditioning stimulus was here changed from the worm solution such as was used in specimens 1–3 to a solution containing 5 grm. of *Mytilus edulis* in 1000 c.c. of sea-water, extracted by grinding with sand and filtering through glass-wool using the vacuum pump. Continuing the

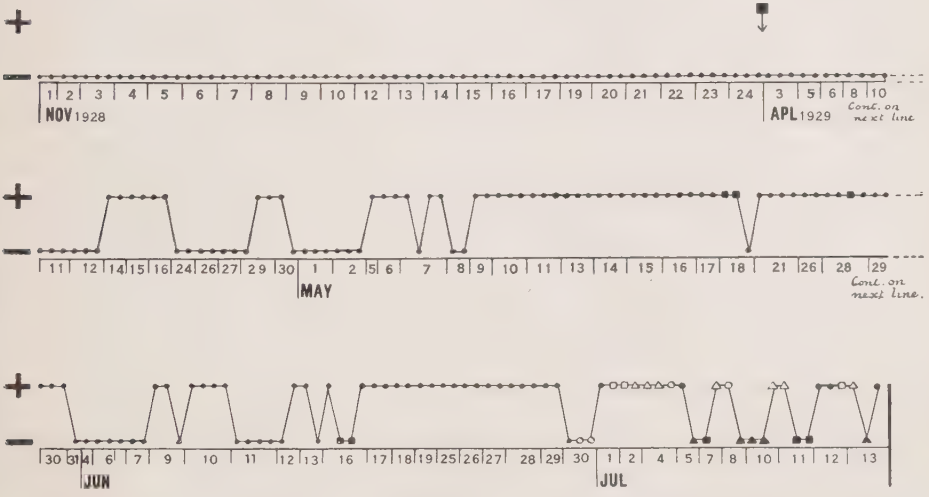

Fig. 10.—Record of the process of formation of a conditioned response in *Blennius pholis* towards *gustatory* stimuli, including also a record of experiments on the same fish with artificial musk. *Specimen* 4. Explanation in text.

Symbols.

Before April 3rd ● = artificial musk.
After April 3rd ● = 0·5% extract of Mytilus.
o = 0·02% ,, ,,
□ = 0·01% ,, ,,
△ = 0·0075% ,, ,,
▲ = 0·00375% ,, ,,
■ = 0·0015% ,, ,,

routine as before, with the 15-second interval between stimulus and food, seventeen associations of this stimulus were required before the first conditioned response was obtained. It was a response however, differing in several important particulars from that shown by any of the specimens of *Blennius gattorugine* investigated at Plymouth. Instead of the direct swimming response to the food place, which was always shown without other motor complications in that species, the response here obtained was made up of a vigorous body movement directed *away* from the opening P (see Fig. 6, P) and towards the incoming taste solution at O. It should be added for those who are not familiar with the habits of these fishes, that

the fish when at rest is usually in a slightly curved position with the tail at O and the head just inside the opening of the home jar ; the curve of the body adapted to fit as close as possible to the hindmost corner (see Fig. 6). When returning to the jar after taking food, the fish enters head-first, but at once turns round and fits itself to this position. So that this complete turn round at the beginning of the conditioned response is a striking movement, especially when accompanied, as it frequently was, by deliberate biting at the incoming solution ! It was also obtained in a parallel experiment on the same species shortly to be described (Specimen 5). There are, I believe, two possible explanations for this new development. (1) That it represents an actual specific difference in the behaviour of the two species ; (2) that the solution of the Mytilus has a different physiological significance to the fish.

It seems hardly likely that the second of these two can be the reason, for it would have been expected that such a movement would result from the stimulus straightway, and without the association with food. It is more probable that it is a true specific physiological difference between the two species, and indicating that *Blennius pholis* has not lost the capacity for unconditioned gustatory response so completely as has *Blennius gattorugine*. I have considered the neurological significance of this reformed gustatory response elsewhere (**3**). It remained a definite feature of the fully formed conditioned response towards the primary stimulus, and is therefore to be regarded as an essential part of it. For this reason, even when not followed by actual movement to the food place, I have recorded in the diagrammatic record as a positive response, all those occasions where this biting and turning response occurred. Practically the whole of the positive results up to May 17th were of this nature. There was a rather lengthy period, from April 12th to May 8th, during which the response gradually became more firmly established. From May 21st onwards the fully formed conditioned response was given invariably in response to the primary stimulus, whilst the biting and turning-back movements continued to precede it.

The effect of external conditions is noticeable at June 4th, 6th, 7th, 9th, and 11th, upon which days there were many disturbances in the room prior to the carrying out of the tests, including loud hammering. On June 29th the tank was cleaned, resulting in inhibition on the following day, June 30th. For all the negative results shown in the record subsequent to May 8th there was a well-defined cause. On June 30th tests were begun to ascertain the extent of generalisation of this stimulus, and the limits of perception. Different symbols are employed in the diagram to denote tests with extracts of different strengths, the details of which are given in the legend.

It is to be seen that by making use of the principle of generalisation of

stimuli, the positive conditioned motor response continued to be given to extracts containing 0·5% (the original and primary stimulus), 0·02% (a plain circle in the record), 0·01% (a plain square), and 0·0075% (a plain triangle), of Mytilus, whilst a consistently negative result was obtained when either of the two following and much lower concentrations was tried,—·00375% (a black triangle), and ·0015% (a black square).

Specimen No. 5. *Blennius pholis*, ♂, 10 cm.

Results in Figure 11.

This experiment was started on June 12th, 1929, the fish having been brought in from the shore that very morning and placed directly in the experimental tank. On the 12th, 13th, and 14th I introduced three times each day 10 c.c. of a solution containing 0·5 grm. of *Patella vulgata* in 100 c.c. of sea-water extracted in the the same way as the Mytilus extract

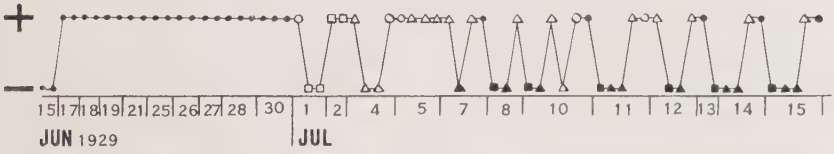

Fig. 11.—Record of the process of formation of a conditioned response in *Blennius pholis* towards gustatory stimuli. *Specimen* 5. Explanation in text.

Symbols.

● = 0·5% extract of Patella.
○ = 0·02% ,, ,,
□ = 0·01% ,, ,,
△ = 0·0075% ,, ,,
▲ = 0·00375% ,, ,,
■ = 0·0015% ,, ,,

used for Specimen 4. This solution formed the primary conditioned stimulus for this experiment. There was no response whatever shown when the above tests were applied.

On the morning of June 15th, 1929, a start was made with the process of conditioning, and the first association made of the Patella solution with food (a small piece of Patella) given 30 seconds later. This interval is a longer one than any yet tried. A second association was made later in the day. On neither of these two occasions was there any sign of the conditioned motor response ; the food when given was fetched, and eaten at once in a typical healthy manner. At the third association of the series, given on the morning of June 17th, I was very surprised to get a perfect response to the Patella solution. Immediately after the solution had begun to enter the jar containing the fish, its head appeared at the opening and exhibited violent gulping movements—an exact replica of those described in Specimen 4 when the response had been perfected. At 10 seconds the fish turned round facing the incoming

solution and biting at it. At 25 seconds it resumed the normal position, and then went straight across the tank to the food-hole where it stayed until food was given at 60 seconds (intentionally delayed). The fish took this at once with great avidity, and returned quickly to the jar. This constituted a record for my experiments in the number of associations required to bring about this type of response, and it was still further remarkable in that it continued to be given throughout the remainder of the experiments without the least hesitation or failure.

It was soon apparent that this specimen was an ideal one for ascertaining the range of perception for such a stimulus by means of the process of generalisation. This was begun on July 1st and the diagrammatic record clearly indicates the strengths of the solutions employed and the resultant responses. The symbols used in the figure represent the same strengths of solution as in the last specimen. It was most interesting to find that the conditioned response failed to occur with the same strengths of Patella extract as the Mytilus extract which was inadequate in Specimen 4, whilst the lowest strength which was able to bring about the response was also the same (0·0075%).

Certain features which were common to the behaviour of both Specimens 4 and 5 appear to have some significance in deciding the *nature* of the perception of this type of stimulus. These concern the appearance of the biting and gulping movements and the sharp turn backwards to bite the incoming extract. I have elsewhere (**3**) concluded that this phase of the total response represents a reformation of the typical *gustatory response* as defined by Herrick (**4**), and which characterises all fishes which at the present time normally seek their food by the aid of gustatory organs. It appears then that this may be built up under experimental conditions, although under their ordinary conditions of living, both of the species of blennies we have investigated have lost this originally dominant sense. In both species also this reformed gustatory response was not obtained at any time when the strength of the extract of Mytilus or Patella used as stimulus was lower than 0·02%, although the characteristic motor response remained unchanged. This would seem to indicate that *olfaction* has been associated with gustatory perception in building up the response, and that in the response to the lower concentrations it (olfactory perception) has taken over the whole or major part of the perception. At the present stage this suggestion is only hypothetical.

Summarising these experiments, it may be said that these fishes, the blennies, are able to form conditioned motor responses towards gustatory stimuli, that the stimulus is capable of wide generalisation, and that the limits for perception of extracts of Mytilus or Patella lie between the strengths represented by the 0·0075 and 0·00375% solutions.

equivalent to an actual stimulation by concentrations slightly less than one-tenth of this.

B. *Results obtained with artificial substances.*

Although I have spent much time at work on this section only one definite result is available, and that of a negative kind. Ultimately a comparison between this section and the last should prove of great interest in defining the exact meaning of gustation and olfaction in fishes.

The object has been to ascertain whether under the same conditions as those of the last section blennies are able to build up the conditioned response to artificial substances, whose concentration in sea-water is such that it can be firmly regarded as a stimulus of a true olfactory nature. A stimulus of this nature is hard to find, for it is very difficult getting such a solution without changing some major factors in the chemical equilibrium of the water. Artificial musk, Trinitro-butyl-toluene, a perfume of cheap soaps, was regarded as fulfilling all requirements. It is not actually soluble to any measurable extent in sea-water, but by adding 1 mgrm. to 1000 c.c. of sea-water, shaking vigorously, and allowing to stand for 24 hours, a solution possessing a highly characteristic and penetrating perfume could be obtained.

By carrying out the experiments in the typical manner, associating the giving of 10 c.c. of this solution with the giving of food 15 seconds later, the result was a totally negative one in all the fishes investigated. Of the fishes used in the last section, and previously used here,

Specimen 2 received 51 such associations over a period of three weeks ;
Specimen 3 received 70 spread over a period of four weeks ; and
Specimen 4, as shown in the first part of Figure 10, was given 64 between November 1st and 24th, 1928.

These experiments taken together provide good evidence that *Blennius gattorugine* and *Blennius pholis* are both unable to perceive this substance in solution when it is presented to them in this manner.

V. GENERAL REMARKS.

A fairly large body of evidence has now been collected by the experiments on visual stimuli. This is sufficient, I think, to enable one to regard the capacity to build up these associations between food and some visual stimulus as general amongst fishes. The experiments on the cod and the coal-fish indicate that the association proceeds just as readily in fishes which under natural conditions do not normally rely so much upon vision as upon other modes of perception, as it does in fishes which do, such as the wrasse and blenny.

It was considered more important to investigate this before proceeding to a finer analysis of vision in one or two species. These experiments are well in hand, and I hope shortly to be able to make a comprehensive statement of visual acuity and colour sense of at least one species of Blennius, and later to contrast it with such a form as Motella, where the role of vision is a very insignificant one in normal life.

In the description of the experiments throughout, many seemingly small details have been mentioned, as I believe them to have value in a final analysis of fish behaviour, and especially when we shall come to a closer comparison of these results with those obtained by a large number of investigators in the dog. This comparison was one of the principal objects of the investigation. In carrying out the work, however, it has become evident that information of more immediate economic application is made possible by the use of this method, so that this aspect is now being given first consideration.

Owing to the length of time taken by these experiments, however, and the great interest of the results for comparative psychology as well as fishery research, it is much to be desired that other workers should take up special aspects of the problem, or work out the finer details in regard to one particular receptor system, such as H. Stetter (**5**) has recently done with the auditory system.

There are many environmental stimuli which are potential governors of fish movement and behaviour, but of whose influence we know absolutely nothing. This is especially so with those factors which have not a direct influence upon the fish, and which cannot in themselves have either a beneficial or a noxious influence. It is for this very reason that it is impossible to ascertain their effect by ordinary methods. Whether the present type of experiment will help, still remains to be seen. The experiments in Section 4 of the present paper lead me to hope that it will. Occasionally difficulties of a perplexing nature arise. In the course of an investigation on the capacity of a cod to form a conditioned response towards an induced temperature gradient in a 10-ft. tank, I had to abandon the test after more than two months' work owing to the fish having taken up a more or less permanent position in the food-box !

VI. SUMMARY.

1. The wrasse, *Crenilabrus melops*, is able to form stable conditioned motor responses to the note of a tuning-fork, sounding the note lower C, or to an electric buzzer giving a mixed note corresponding to the note F in the second octave, when either of these is used singly. In a discrimination test employing both these sounds the wrasse was not able

to distinguish between them as sounds, but differentiated them by their position.

2. Conditioned responses involving visual stimuli have been built up in the following additional species : plaice, cod, and coal-fish. Individual variations in the response are described.

3. *Blennius gattorugine* and *Blennius pholis* are able to form stable conditioned responses towards gustatory stimuli such as sea-water extracts of natural food substances. These stimuli are widely generalised in their action. The limits for perception lie between concentrations slightly less than 0·000375% and 0·00075% of the weight of living food substance in sea-water. Many significant details in the responses are described and discussed.

These fishes do not appear to be able to respond to an artificial olfactory stimulus such as artificial musk.

4. The essential similarity between these responses and conditioned reflexes in dogs is becoming more emphasised as the data accumulate.

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The Vertical Distribution of Marine Macroplankton. IX. The Distribution of the Pelagic Young of Teleostean Fishes in the Daytime in the Plymouth Area.

By

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Naturalist at the Plymouth Laboratory.

With 7 Figures in the Text.

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INTRODUCTION.

In continuation of the study of the vertical distribution of the pelagic young of Teleostean fishes, already reported on for 1924 and 1925 (**1**), a further fifteen stations were made with the two-metre stramin net in the daytime between April and September in 1926. The collections were made in a manner exactly similar to that for those of the previous years, hauls of ten minutes' duration being made almost always at six different depths with the net towed horizontally as near as possible at the same speed on each occasion. The Admiralty depth-recording instrument was used at every station, and the results for each haul are given in Figures 6 and 7 on pages 666 and 667, which show the graphic records of the path of the net through the water for each haul. (That for June 25th is not included, an unsatisfactory record being obtained on that day owing to the drum of the recorder not having been fully screwed down, see **4**, p. 431.)

Nearly all the collections were made in the same locality, namely, about two miles east of the Eddystone Lighthouse, in water of a depth of about 54 metres. (This position is known in this and previous papers as "A".)

The full details as to the time of day, weather conditions, depths of hauls, etc., are given in the log on page 668 at the end of the report.

Previous research had indicated that possibly some species may have lived in the daytime in water layers nearer the bottom than had been sampled by the ring-trawl. Accordingly the work has been supplemented in 1927 and 1928 by collections made with the bottom plankton net described in a previous publication (**5**), and, for comparison, oblique hauls made with the two-metres ring-trawl fishing in the water layers from a depth of about 35 metres up to the surface itself. In making the oblique hauls the net has been fished at six different depths using exactly the same lengths of wire as have been used for the serial hauls in the previous years. The net was fished for five minutes at each depth, the necessary amount of wire being wound in after that period until the six depths including the surface had been fished. On two occasions the depth recorder was in use, and Figure 1 shows the path of the net through the water on these occasions. In the first case, June 29th, 1927, the maximum depth reached was 30 metres, and on July 8th, 1927, it was 46 metres. These depths probably represent the limits within which the maximum depth reached on each occasion lies: in all the previous collections to study the vertical distribution of the plankton, the maximum depth of the deepest haul has usually been between these depths. When possible the collections with the bottom plankton net and those of the oblique hauls were made on the same day, one haul being made with the ring-trawl at Station A, and three with the bottom net, viz. at A, at the International Hydrographic Station L4, and at a position about 2 miles W.S.W. of the

Rame Head on a muddy bottom. Altogether 36 oblique hauls with the ring-trawl and 114 hauls with the bottom plankton net were made. The data for these catches are necessarily bulky and are not being published; they have been carefully examined, and it is considered sufficient for the present purpose that they should be given as in Tables 5 and 6, pages 675–6, namely, as average monthly catches only. The total number of fish caught in any one month has been divided by the total number of hauls for that month. On page 642 are given the dates

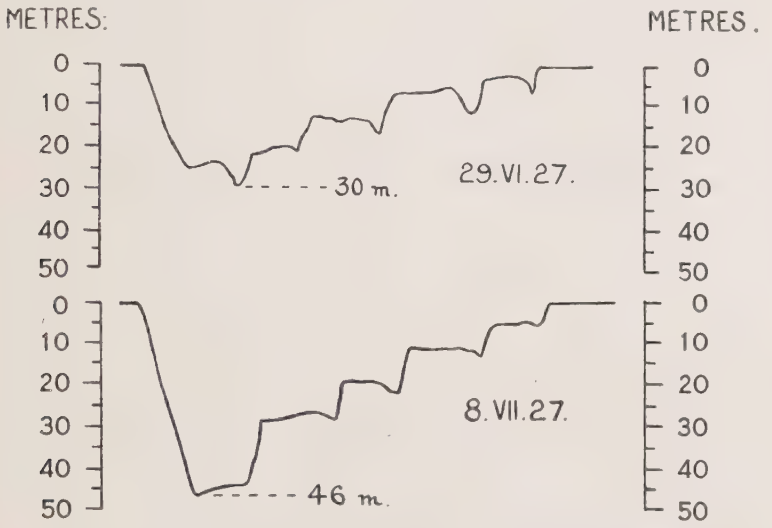

FIG. 1.—Tracings given by the depth-recorder indicating the path of the ring-trawl through the water for the half-hour oblique hauls on June 29th, 1927, and July 8th, 1927. The net enters the water on the right-hand side of each curve.

on which the various collections were made. All the collections were made in daylight.

In compiling Table 5, giving the average monthly catches for the bottom plankton net, the actual figures have been multiplied by 8·5 to bring them as nearly comparable to the oblique ring-trawl figures as possible. The bottom plankton net was so constructed that the area of its mouth was 1/8·5 that of the two-metre ring-trawl (**5***, p. 107).

It is with pleasure that I acknowledge my indebtedness to Capt. V. Lord and the crew of the s.s. *Salpa* for their co-operation and assistance in making the collections.

* I am greatly indebted to Mr. J. S. Colman for pointing out an error in this publication (**5**, p. 107). In line 23, "fishing area" should read "circumference," and in line 25, "a quarter" should read $\frac{1}{8\cdot5}$: on the following pages, therefore, 8·5 should be read in place of 4 on each occasion and the necessary corrections made.

Dates of Collections with Ring-trawl and Bottom Plankton Net.

	Bottom-stramin net, 30-minute hauls at three different stations.	Ring-trawl, 30-minute oblique hauls 2 miles East of the Eddystone.
1928.	January 3, 11, 17, 26	January 9, 16, 26, 30
	February 3, 10, 14, 24, 29	February 2, 20, 27
	March 8, 23, 30.	March 5, 21, 30
	April 12, 18, 23, 24, 30	April 4, 11, 12, 23
	May 11, 17	—
1927.	June 2, 29	June 2, 9, 29
	July 8, 15	July 8, 12, 21, 26
	August 5, 12, 19, 25, 31	August 4, 8, 19, 26, 31
	September 6, 15, 20, 30	September 6, 15, 19
	October 4, 13, 18, 25	October 4, 13, 18, 24
	November 1	November 1
	December 6, 15, 21	December 15, 21
	114 hauls.	36 hauls.

GENERAL RESULTS.

The general results of the above collections have confirmed and extended those previously published. There can now be no doubt that the different species of fish differ markedly in the depths at which their post-larvæ are to be found most abundantly in the daytime in the waters off Plymouth.

It would appear to be possible to place our post-larval fishes under the following headings as regards their vertical distribution in the daytime on a sunny day in waters of 50 metres depth off Plymouth during the months in which they are most abundant. When a note of interrogation (?) appears after the name of a fish, it implies that the number of individuals caught of that species are not sufficient to be considered significant, and the indications only are that the fish may come under the category in which it is placed.

Most abundant from surface layers down to 5 to 10 metres.

Gadus pollachius (Pollack); *Blennius gattorugine* (Tompot Blenny); Labridæ (Wrasses); *Rhombus* sp. (Brill and Turbot) (?).

Abundant at all depths, but mostly above 25 to 30 metres and sometimes avoiding the actual surface.

Onos sp. (Rockling); *Arnoglossus* sp. (Scaldbacks); *Scomber scomber* (Mackerel); *Trachinus vipera* (Lesser Weaver); *Caranx trachurus* (Horse Mackerel).

Abundant below 15 metres, and falling off in numbers below 30 to 35 metres.

There is a tendency for the following species which come under this category to show slight differences in their preference of depth, becoming successively deeper in the following order (see Fig. 2) :

Scophthalmus norvegicus (Ekstrom's Topknot) ; *Pleuronectes flesus* (Flounder) (?) ; *Gadus merlangus* (Whiting) ; *Solea vulgaris* (Sole) (?) ; *Pleuronectes limanda* (Dab) ; *Solea variegata* (Thickback) ; *Trigla* spp. (Gurnards) ; *Callionymus* sp. (Dragonets), deeper in June and July than in April and May ; *Pleuronectes microcephalus* (Merrysole) ; *G. luscus* (?) (Pouting) ; *Molva molva* (Ling) (?) ; *Merluccius merluccius* (Hake) (?) ; *Zeugopterus punctatus* (?) ; *Lebetus scorpioides* (?).

Becoming abundant below 20 to 25 metres, with maximum abundance probably very near bottom.

Gadus minutus (Bib or Poor Cod) ; *Gobius* spp. (Gobies) ; *Lepadogaster bimaculatus* (?) ; *Cottus bubalis* (Bullhead) (?).

Irregular in their type of distribution, though usually avoiding the actual surface.

Clupeid spp. (Sprat and Pilchard), when present in daytime ; *Ammodytes* spp. (Sandeels).

A certain elasticity must be allowed in a scheme like this where one is dealing with a population of living animals in their natural environment ; but it seems legitimate to say that on a clear sunny day, with the sea surface calm, just before midday, such would be the vertical distribution of the post-larvæ of the above fish in water of 50 metres depth off Plymouth in the months when the respective fish are most abundant.

An average vertical distribution, in the case of those species whose post-larvæ have been numerously represented in the collections on several occasions, has been estimated by superimposing all the diagrams so far obtained giving the actual vertical distribution of the fish in question on sunny days ; that is, by tracing through, one over the other, each vertical distribution diagram that has been obtained. From this superimposition of figures an average vertical distribution for the species has been drawn freehand and is shown in Figure 2. The accuracy of these diagrams has been checked by working out the average catch of each fish on sunny days for every five metres depth from the total of all the collections made in 1925 and 1926. On the top half of Figure 2 are given the vertical distribution diagrams which can be expected on sunny days during the months of April and May for the commoner species found here whose chief spawning period lies in the spring. On the lower half of the figure similar diagrams are given for the vertical distribution of the post-larval stages of those whose spawning period lies in the summer months and whose post-larvæ are most abundant in June, July and August. The data for these

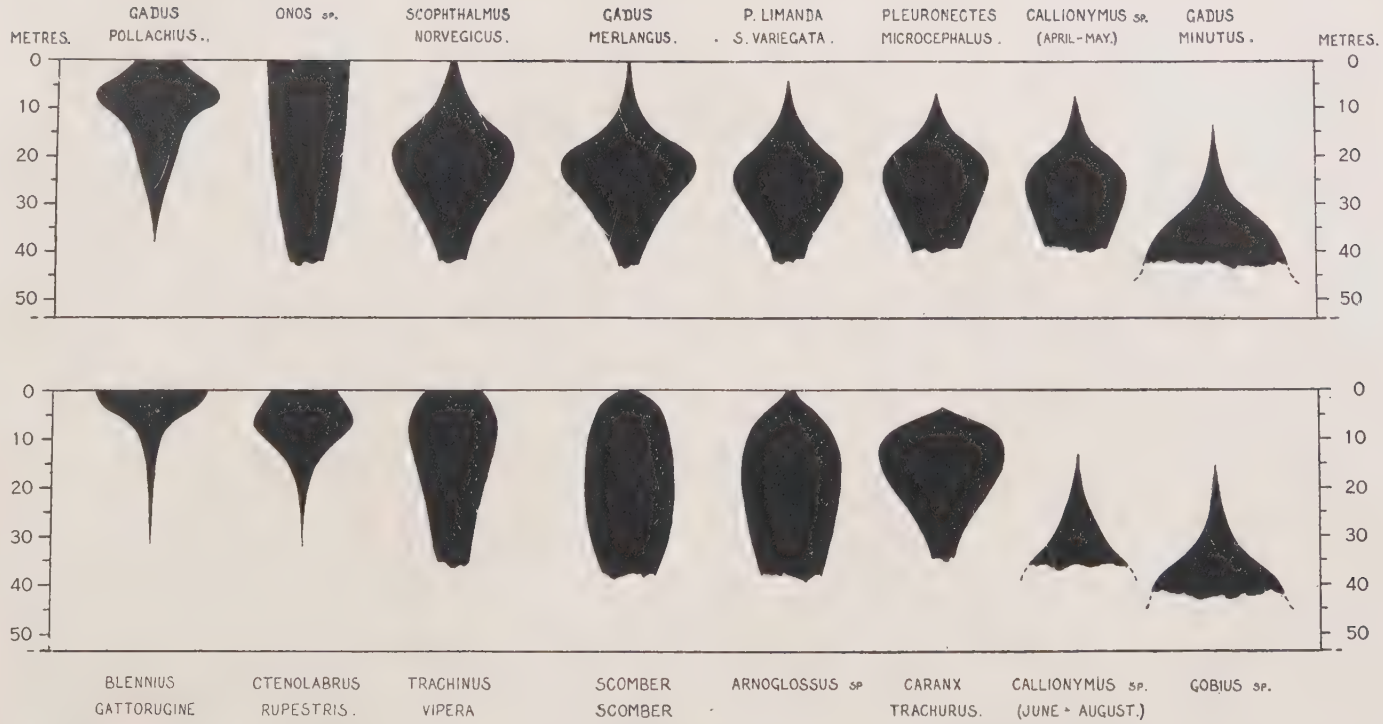

FIG. 2.—Average vertical distribution for the post-larvæ of the above species during the months when they are most abundant on sunny days just before noon in water 54 metres deep off Plymouth. The upper half shows the expected vertical distribution for the post-larvæ of certain spring-spawners; while the lower half shows that for some summer-spawners.

latter are by no means so definite as are those for the post-larval stages of the spring spawners ; the numbers of times on which they have been taken in sufficient numbers to give significant results are few, and in one or two cases (e.g. *Trachinus vipera* and *Caranx trachurus*) the figures are based on one result only. It is a general rule that the summer forms are not nearly so abundant as the spring forms.

While the above scheme can be taken as holding for the conditions stated, namely, a sunny day before noon, with a calm sea, there are certain factors which operate to affect such distributions under the same conditions, and other conditions which give rise to changed distributions during the day and from one day to the next. These factors are :—

1. Dull weather.
2. Time of day.
3. Abundance of other plankton organisms.
4. Nearness to coast.

1. *Dull weather.* There are definite indications that in dull weather certain species of post-larvæ are higher in the water than on sunny days. While the number of observations made on dull days are fewer than those made on sunny days, there is nevertheless a certain consistency to be found in the results.

For example, in Figure 4, page 658, the upward trend in the vertical distribution of Callionymus post-larvæ can be seen between the days April 22nd (Sunny) and April 26th (Dull), as also between May 6th (Sunny) and May 19th (Dull) ; the same also can be seen for other species of fish in this and the previous paper (**1**).

2. *Time of day.* The majority of the observations recorded here represent the results of collections made between the hours of 10 a.m. and 12 noon (G.M.T.) (see List of Stations, p. 668). Figures 3, page 652, and 4, page 658, show, however, in the case of *Gadus merlangus* post-larvæ and of those of Callionymus the vertical distribution at two periods during the day. On April 13th, 13.iv.26 (i) represents the results of the collections made between 11.3 a.m. and 12.38 p.m., while the 13.iv.26 (ii) hauls were between 1.40 p.m. and 2.51 p.m. ; the surface haul was taken in the first case at 11.3 a.m. and in the second at 2.51 p.m., and the bottom hauls at 12.38 p.m. and 1.40 p.m. respectively. It can be seen that there has been a quite definite, though slight, move upwards in the vertical distribution of these species between the morning and afternoon observations.

Any alterations caused by the passage from daylight to darkness have been recorded in previous papers (**2** and **3**).

3. *Abundance of other plankton organisms.* There have on several occasions been indications that certain changes in the normal vertical

distribution of post-larval fishes may be found correlated with extreme abundance of certain other plankton animals in the surface layers.

The following occasions have already been recorded. On May 19th, 1925 (**1**, p. 109), the occurrence of post-larvæ of *Gadus merlangus*, *Scophthalmus norvegicus*, *Solea variegata*, and *Callionymus* sp., at the surface was noticed to coincide with the presence of a dense swarm of the megalopas of *Corystes cassivelaunus* in the surface layers. In another locality on the same day, where the megalopas were scarce in the surface layers, the post-larvæ of the above-mentioned species exhibited a normal vertical distribution.

On June 4th, 1926 (**3**, pp. 833 and 841), post-larvæ of *Scophthalmus norvegicus*, *Solea variegata*, and *Callionymus* sp., were very much higher in the water than on the previous day; this was correlated with the presence of very dense swarms of *Calanus finmarchicus* in the surface layers.

On August 4th, 1926, the numbers of post-larvæ taken in the surface layers were unusually large, and on this day the swarms of Calanus on the surface were exceptional (**4**, p. 432).

4. *Nearness to coast.* It has already been shown (**1**, p. 108) that "the post-larvæ of many species of fish become abundant at much smaller depths below the surface close inshore over shallow water than they do a few miles from the coast over depths of 50 metres or more."

The Difference in Behaviour Between Post-larvæ of Spring and of Summer Spawners.

Figure 2 shows up a very striking general result that has arisen from the observations of 1926 supplemented with those of previous years. This is that there appears to be a fundamental difference between the behaviour of the post-larvæ of the spring spawners and that of the post-larval stages of the summer spawners. While the majority of the post-larvæ of spring spawners (with the exception of those of *Gadus pollachius* and of *Onos* sp.) tend to be below 15 metres in the daytime with their maximum numbers at 20 metres or deeper, those of the summer spawners seem to prefer the upper layers and are usually most numerous above 25 metres, except such forms as *Gobius* spp. and *Lepadogaster bimaculatus*.

The significance of this is not understood. The summer spawners are mostly representatives of warm-water fish on whose northern limit of distribution this region lies or whose distribution is affected by the movements of the warm waters of the Gulf Stream Drift. Possibly in the latitudes in which they are most prevalent they live deeper, although, owing to the greater sunlight in those latitudes, they may experience normally higher intensities of light than do the cold-water forms in their normal

habitat. These intensities are only to be found in the upper layers in this region. On the other hand, it may be that the preference for the upper layers is conditioned by temperature, and in these layers the highest temperatures are to be found.

A Comparison between the Catches of the Bottom Plankton Net and those of the Oblique Hauls with the Two-metre Ring-trawl.

Between June, 1927, and May, 1928, 114 hauls were made with the bottom plankton net, and 36 oblique hauls with the two-metre ring-trawl. The results of these catches have been expressed in Tables 5 and 6, pages 675 and 676, as average monthly catches (see p. 643) ; in these tables the 1928 hauls have been placed before those of 1927 so that the results show conveniently the sequence of a regular calendar year. Unfortunately in 1928 there were no oblique-haul collections made during the month of May ; in the table, however, are given for that month the average half-hourly catches for the five years 1924, 1925, 1926, 1927, and 1929.

During the course of the researches on the vertical distribution of plankton it had become evident that certain forms, e.g. Clupeid post-larvæ and *Tomopteris helgolandica*, were not being taken in numbers in the daylight catches although night collections showed that they were really present in abundance in the region investigated. The natural conclusion was that such forms lived in the daytime in layers deeper than those normally sampled by the ring-trawl, that is somewhere between 35 metres and the bottom at about 54 metres. In order to obtain definite evidence on this point the net described in a previous publication (**5**) was employed.

The area of the mouth of the ring-trawl was 8·5 times that of the bottom plankton net, and the results shown in Table 5 are therefore the actual results multiplied by 8·5.

In most cases where the normal distribution has been shown by previous ring-trawl collections to be well up in the water it would be expected that the comparable bottom plankton net hauls would provide catches less than, or at any rate never greatly exceeding, those of the obliquely-hauled ring-trawl. Such has proved to be the case when the species in question have occurred in the catches in sufficient numbers to give significant results. Those forms which normally live high in the water up to the surface layers naturally appeared in far fewer numbers in the bottom plankton net than in the oblique hauls, e.g. *Gadus pollachius* post-larvæ were 25·9 times more numerous in the oblique hauls than in those of the bottom net, and in the case of *Scomber scomber* this figure was 7·3.

It has already been pointed out that the post-larval sprats and pilchards became ten to thirty times as numerous in the dark as in the daytime in the ring-trawl catches (**3**, p. 835), and in the 24-hour series of observations made in 1926 there were indications that these Clupeids moved down to levels below those sampled in the daytime. It was hoped, therefore, that the results of the collections with the bottom stramin net might settle this point. Examination of Table 6, page 676, shows, however, that the average catch for any month with the oblique ring-trawl sometimes exceeds, and sometimes is less than, that with the bottom plankton net, the total number for the year being approximately the same in the ring-trawl as in the bottom net. The evidence that the post-larval clupeids seek the actual layers next to the bottom is therefore negative. The possibility remains that they do not actually hug the bottom, but swim two or three metres above it, in which case a net with a much deeper mouth must be employed. There is one other possible explanation for their absence in the daytime catches, that is that in the daytime they are shoaling and only if the net actually passes through a shoal will the post-larvæ appear in any quantity in a catch ; whereas at night the shoals break up and certain numbers are bound to be caught in all layers (**2**, p. 401).

While these researches have not definitely furthered our information on the habits of post-larval Clupeids, they have produced striking evidence on the behaviour of two other kinds of fish, namely, the post-larvæ of *Gadus minutus* (the Bib or Poor Cod) and those of *Gobius* spp.

Previous daylight observations on the vertical distribution of *Gadus minutus* showed that they lived always below about 30 metres. The fact also that at the lowest depths sampled their numbers were still increasing indicated that possibly the region of maximum abundance lay still deeper and had not been sampled. The results with the bottom plankton net show that, while the smaller post-larvæ are about as numerous near the bottom as they are in the oblique hauls, those of 12 mm. length and over have congregated in great numbers right close to the bottom itself.

In a previous paper (**1**, p. 108) it had been pointed out that the post-larval Gobies in the collections in 1925 were extremely few compared with those of 1924, and it had been suggested that they were indeed scarce that year. Night observations showed, however, a considerable increase in their numbers, and the results of the bottom plankton net have revealed their presence quite close to the bottom in the daytime in great quantities. Rather similar results were shown also for post-larvæ of *Lepadogaster bimaculatus* although their numbers were very much smaller.

In the foregoing pages are briefly given the observations for each species for the recent collections and the conclusions drawn from these and the previous collections already published (**1**, **2**, and **3**). In Tables 1,

2, 3, and 4 at the end of the paper are to be found the numbers of fish of each species caught during the course of the investigations.

CLUPEIDÆ.

Clupea sprattus L. (Sprat) and Sardina pilchardus (Walb.) (Pilchard).

Figure 4, page 658, shows the results of the vertical distribution observations for these species in 1926; while the earlier catches can be taken to consist mostly of sprat, those of the later months will be mostly pilchard.

These observations confirm the previous conclusions that these post-larvæ, 4–20 mm. long, when caught in the daylight appear to be distributed rather indiscriminately. At the same time, series of observations which have been made at night (**2** and **3**) show that the daytime distribution cannot be a true picture of the habits of the majority of these Clupeid post-larvæ since they increase in number 10 to 30 times in the catches at night.

It was hoped that the results of the bottom plankton net collections would throw light on this question by showing an increased number in the bottom layers. Tables 5 and 6 (pp. 675 and 676) show, however, that while in six months in the year more were taken in the ring-trawl oblique hauls than in the bottom plankton net, in the other six months the reverse was the case. Actually, taking the total of the monthly averages for the year, approximately the same number were taken in the ring-trawl as in the bottom plankton net, and in June and July, the months in which a marked increase in numbers has been shown in the upper layers at night, there were 9 and 10·6 times as many in the ring-trawl as on the bottom. It should here be mentioned that the post-larvæ occurring in the catches from January to the beginning of March will be mostly those of *Clupea harengus*, the Herring, and there is perhaps an indication in the March hauls of their being near the bottom; but in this case, and in other months when the bottom plankton net catches exceed those with the ring-trawl, nothing like the striking differences were found as were shown in the case of *Gadus minutus*, the Gobies, or *Lepadogaster bimaculatus*.

It would therefore seem that the true behaviour of Clupeid post-larvæ remains yet to be shown. It is possible that the bottom plankton net samples too narrow a layer above the bottom and that some net fishing a metre or more above the sea bottom may show the presence of these young fish in abundance in the daytime. Alternatively, as mentioned above on page 648, the post-larvæ may shoal in the daytime, the shoals breaking up at night.

GADIDÆ.

Gadus pollachius L. (Pollack).

In the 1926 collections few only of this species were taken, and these indiscriminately at all depths. There was no evidence that they avoided the surface layers, and the conclusions based on these and the previous observations would seem to be that they may be taken at all depths, but are on the whole more numerous actually in the surface layers. The post-larvæ in question are from 4 to 10 mm. in length.

The collections in the oblique hauls with the ring-trawl in April, 1928, showed a fairly high average of 21·6 specimens per haul against the low average of 0·9 in the bottom plankton net, confirming that they are not abundant in the layers near the bottom.

Gadus merlangus L. (Whiting).

Figure 3 shows diagramatically the results of the 1926 collections. They confirm the conclusion previously stated that the majority of whiting post-larvæ, 5 to 12 mm. in length, live below 15 metres, although the seasonal change suggested in the previous report was not shown so markedly. The rise of these young fish in the water on May 19th is no doubt due to the fact that the day was very dull.

All results can be summarised as follows :—

Post-larvæ 5–12 mm. mostly below 15 metres ; region of maximum abundance 20 to 30 metres, falling off in numbers considerably below 35 metres.

Post-larvæ 12–50 mm. in association with Cyanea, living at the depths that the Cyanea are in the daytime and following their migrations at night.

Ratio oblique hauls with ring-trawl : bottom plankton net=7·5 : 1.

Gadus minutus (O. F. Müll.) (Bib or Poor Cod).

The 1926 results (Figure 3) confirm the fact that post-larvæ of the poor cod, 4–10 mm. in length, are the deepest living of the common Plymouth gadoids, being most abundant almost always well below 20 metres.

Further light is shown on their behaviour by the collections made with the bottom plankton net. Below are given the numbers caught in half-hour oblique hauls with the ring-trawl and the average catches for three half-hour hauls on each day with the bottom plankton net.

Ring Trawl (Oblique).		Bottom Plankton Net.*	
February 27th	12	February 29th	–
March 5th	29	March 8th	36·6
,, 21st	14	,, 23rd	17
,, 30th	30	,, 30th	385·1
April 4th	166	April 12th	229·5
,, 11th	120	,, 18th	133·5
,, 23rd	65	,, 23rd } ,, 24th }	138·6
		,, 30th	3689
		May 11th	3034·5
		,, 17th	325·6

It can be seen from the above figures that up to April 23rd the numbers of post-larval poor cod taken in the bottom plankton net are on the whole greater than those taken in the oblique hauls with the ring-trawl, but after that date there is an enormous increase in the numbers caught in the bottom net, though unfortunately there are no catches with the ring-trawl for comparison.

An examination of the following table, which gives the lengths in millimetres of the fish taken on various dates, shows very definitely that this increase in numbers is due to a sudden descent to the bottom of fish from the layers above.

Length in millimetres.

		4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
March 30th	B.N.	–	5	14	9	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
April 12th	B.N.	2	5	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
,, 18th	B.N.	–	1	2	5	3	–	1	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–
,, 25th	B.N.	–	1	4	7	3	2	4	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
,, 23rd	R.T.	–	1	4	10	8	13	5	–	2	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–
,, 30th	B.N.	–	–	–	–	–	–	–	1	–	2	2	7	13	24	34	27	20	11	4	3	3	3	5	1
May 11th	B.N.	–	–	–	–	–	–	2	1	3	13	19	32	38	36	18	12	3	1	1	–	–	–	1	–
,, 17th	B.N.	–	–	–	–	–	2	1	3	3	4	2	4	5	4	3	1	2	–	–	–	–	–	–	–

B.N. = Bottom Plankton Net. R.T. = Ring-trawl.

In all previous collections it appears that the post-larval poor cod disappear from the catches at a length of between 10 and 12 mm. In the previous publication (**1**, p. 119) it is said, "The majority of post-larvæ caught were between 5 and 10 mm. in length, and there is no evidence of any differentiation in the distribution of the various sizes within these lengths ; for those above 10 mm., however, there is an indication that they live deeper down."

Here we have definite evidence that there is a sudden descent of the young fish to the layers immediately above the bottom soon after the

* Average of catches at three stations on each day, multiplied by 8·5 for comparison with ring-trawl.

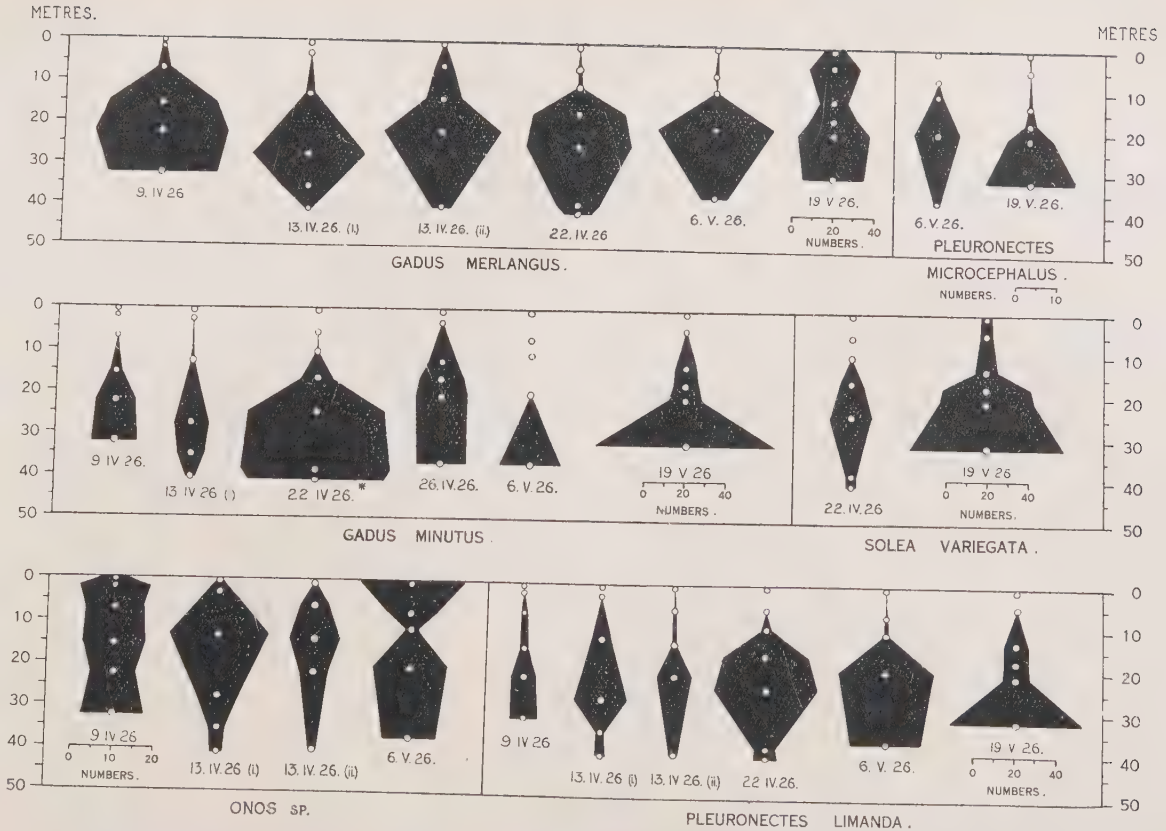

FIG. 3.—The vertical distribution of post-larvæ of the above species on the dates given. The white spots and black circles indicate the "average depths" at which hauls were taken. **Gadus minutus*, on 22. iv. 26, is drawn to half the scale of the others.

fish has reached 10–12 mm. in length ; the majority of fish in the bottom net catches on April 30th were between 12 and 21 mm. long, and the largest was 27 mm. It is possible that above this length they are fully able to avoid capture by the slow-moving net.

Summary of results :

Post-larvæ 4–12 mm., chiefly in water layers between 20–25 metres and the bottom.

Post-larvæ 12–27 mm. in water layers immediately above the bottom.

Ratio, oblique hauls with ring-trawl : bottom plankton net=1 : 13·9.

Gadus luscus L. (Pouting).

Post-larvæ of this species were not abundant in the 1926 catches, the main breeding period lying possibly between December and April. Altogether 74* post-larvæ, mostly between 4 and 8 mm. long, were taken, and of these one was taken from between the surface and 10 metres, 9 between 10 and 20 metres, 34 between 20 and 30 metres, and 30 between 30 and 41 metres, confirming the 1925 results which pointed to the post-larvæ of the pouting being deep-living.

Ratio, oblique hauls with ring-trawl : bottom plankton net=1·8 : 1.

Gadus callarias L. (Cod).

A few post-larvæ of the cod, 5 to 8 mm. in length, occurred in the catches during April in 1926, but the numbers were too low to be significant. Altogether 4 specimens were taken above 10 metres, 9 between 10 and 20 metres, 3 between 20 and 30 metres, and 5 between 30 and 41 metres, the largest catch being 8 at 15·5 metres on April 9th.

Onos sp. (Rockling).

Figure 3 shows the results of the collections in 1926. These confirm the previous conclusions that Onos post-larvæ are to be found at all depths with a slight preference for the surface layers. The post-larvæ in question are 4–10 mm. in length, and after this size they are to be found always in large numbers congregated under masses of drifting weed.

Ratio, oblique hauls with ring-trawl : bottom plankton net=4·1 : 1.

Molva molva L. (Ling).

Only a few post-larvæ of this species were taken, but these were all but one from below 15 metres ; this confirms the previous observations.

None were taken in the bottom plankton net.

* On this and all succeeding occasions the numbers taken in the daylight on June 3rd–4th are included (**3**, Table X, p. 850) although they are not repeated in Table 2.

Merluccius merluccius L. (Hake).

Post-larvæ of the hake were only taken on July 26th, 1926, when 4 specimens, 4 to 5 mm. in length, were caught, 2 at 18·5 metres, one at 28·7 metres, and one at 35·1 metres ; and on June 3rd, when one specimen, 5·5 mm. long, was taken at 31·5 metres.

Ratio, oblique haul with ring-trawl : bottom plankton net=1·9 : 1.

Raniceps raninus L. (Lesser Forkbeard).

Only five post-larvæ of this species, 4–6 mm. in length, were caught in 1926, one at 43·1 metres on June 25th, two at 40·7 metres on July 13th, and one each at 21·5 and 34·1 metres respectively at E1 on July 15th.

No post-larvæ of this species appeared in the bottom plankton net.

CAPROIDÆ.

Capros aper L. (Boarfish).

Four post-larvæ only of this species were taken ; one of 3½ mm. from 13·7 metres at E1 on July 15th, and three of 4–4½ mm. from 22·2 metres on August 4th.

No post-larvæ of this species appeared in the bottom plankton net.

BOTHIDÆ.

Arnoglossus sp. (Scaldbacks).

Figure 5, page 662, shows the results for Arnoglossus sp. post-larvæ, probably *A. laterna* (Will), on the three days on which they were at all numerous ; but on this occasion, and in the previous year, the numbers were not great enough to allow conclusions to be drawn with safety. The indications are, however, that post-larvæ, 6 to 20 mm. long, may occur at any depth, but there is generally a tendency to avoid the actual surface layers down to a depth of about 5 metres.

Ratio, oblique hauls with ring-trawl : bottom plankton net=2·2 : 1.

Rhombus spp. (Turbot and Brill).

Post-larvæ of these species, *Rhombus maximus* Will. and *R. lævis* Rond., were never very numerous, but the indications were definitely that they preferred the upper layers above 10 metres and actually at the surface itself. Altogether 36 specimens were caught between the surface and 10 metres, 9 between 10 and 20 metres, one between 20 and 30 metres, and 5 between 30 and 40 metres. No post-larvæ of these species occurred in the catches of the bottom plankton net.

Scophthalmus norvegicus (Günther), (Norway Topknot).

The only occasion on which this species was present in anything like its usual abundance was on June 3rd, 1926, when its distribution has already been reported (**3**, p. 841). The small numbers caught on all other occasions, however, confirm the previous conclusions that post-larvæ, 4 to 10 mm. in length, usually occur in greatest abundance below about 10 metres, being most numerous between 15 and 30 metres.

Ratio, oblique hauls with ring-trawl : bottom plankton net = 1·2 : 1.

Zeugopterus punctatus (Bloch.).

Only very few post-larvæ of this species were taken ; on April 13th, one each at 21·6 and 40·1 m. ; on April 22nd, one at 16·9 m. and four at 24·6 m. ; on April 26th, one at 12·6 metres and one at 16·7 metres ; on May 6th, two at 37·1 metres, and on May 19th, two at 17·6 metres and six at 32 metres. On June 3rd and 4th, 29 were caught, all below 10 metres depth. This confirms previous observations that these post-larvæ occur usually only below 10 metres and deeper.

Ratio, oblique hauls with ring-trawl : bottom plankton net = 2·5 : 1.

PLEURONECTIDÆ.

Pleuronectes limanda L. (Dab).

Figure 3 and the results given in Tables 1–4 confirm the previous conclusions that post-larval dabs, 5–13 mm. in length, occur most abundantly below a depth of 15 to 20 metres.

Ratio, oblique hauls with ring-trawl : bottom plankton net = 1·9 : 1.

Pleuronectes microcephalus (Don.), (Merrysole).

Figure 3 and the results given in Tables 1–4 confirm the previous conclusions that post-larval merrysoles, 4–13 mm. in length, occur most abundantly below a depth of 15 to 20 metres.

Ratio, oblique hauls with ring-trawl : bottom plankton net = 1·7 : 1.

Pleuronectes flesus L. (Flounder).

Post-larvæ of the flounder, 4–9 mm. in length, were not very numerous in the catches, and of the total number caught 7 were from between the surface and 10 metres, 25 between 10 and 20 metres, 17 between 20 and 30 metres, and 13 between 30 and 41 metres. Thus it would seem that these post-larvæ occur slightly higher in the water than those of the dab, being already comparatively abundant at 10 metres.

Ratio, oblique hauls with ring-trawl to bottom plankton net = 4·5 : 1.

SOLEIDÆ.

Solea variegata (Don.), (Thickback).

Post-larvæ of the thickback, 4–10 mm. in length, as shown by Figure 3 and previous records have a vertical distribution similar to that of the dab, becoming most abundant below a depth of 15–20 metres.

Ratio, oblique hauls with ring-trawl : bottom plankton net = 4 : 1.

Solea vulgaris (Quens.), (Common Sole).

As in the previous year's collections the post-larvæ of the common sole were never very abundant in the 1926 catches. The largest catches were on April 22nd, when the majority lay below 10–15 metres.

Ratio, oblique hauls with ring-trawl : bottom plankton net = 1 : 3·7.

Solea lascaris Risso. (Sand Sole).

Only one post-larva of this species, 6·5 mm. in length, was taken, this being from 20·1 metres on July 13th. None were taken in the bottom plankton net.

SERRANIDÆ.

Serranus cabrilla L. (Sea Perch).

Three post-larvæ of this species occurred in the catches ; one of 6 mm. from 13·7 metres at E1 on July 15th, and two of $4\frac{1}{2}$ and 5 mm. from 3·5 metres on August 4th.

CARANGIDÆ.

Caranx trachurus (L.), (Horse Mackerel).

Post-larvæ of the horse mackerel, 4–15 mm. in length, only occurred in any numbers on August 4th (Fig. 5, p. 662). On this occasion while they were numerous at depths below 20 metres the greatest catch was from 9·5 metres. This seems to confirm the previous indications that the majority of the post-larvæ of this species are to be found above 20 metres. None were taken in the bottom plankton net. Below are given the actual sizes of the post-larvæ caught at each depth on August 4th. It can be seen that while the majority were between 4 and 10 mm. in length, at 9·5 metres there were a few larger specimens up to as much as 15 mm., although these were absent from other depths. In the same table are given the sizes of four of the medusa, *Cyanea capillata*, that were caught at the same time in the upper layers, and it seems very probable that the larger post-larvæ at 9·5 metres were in association with the large Cyanea which was 6 inches in diameter.

August 4th, 1926	Length in millimetres.												Cyanea.
	4	5	6	7	8	9	10	11	12	13	14	15	
Surface (ii)	–	5	2	–	–	–	1	–	–	–	–	–	2″
3·5 m.	–	–	–	1	–	–	–	–	–	–	–	–	3″
9·5 m.	1	2	15	20	20	12	13	9	12	3	3	1	6″ : 3″
22·2 m.	–	5	7	5	2	1	–	–	1	1	–	–	–
28·2 m.	–	16	13	8	1	–	–	–	–	–	–	–	–
39·4 m.	1	23	13	5	–	–	–	–	–	–	–	–	–

SCOMBRESOCIDÆ.

Belone vulgaris Flem. (Garfish).

One post-larval garfish, 22½ mm. long, was taken at the surface on August 4th.

AMMODYTIDÆ.

Ammodytes tobianus L. (Lesser Sandeel).

Post-larvæ of this species were taken in too small numbers to give a significant picture of their distribution, though the indication was that they showed no definite preference for any depth.

Ratio, oblique hauls with ring-trawl : bottom plankton net=1·5 : 1.

Ammodytes lanceolatus (Lesauv.), (Greater Sandeel).

Post-larvæ of this species, 5–20 mm. in length, were never very abundant, but what evidence there was confirmed the previous conclusions that they are somewhat irregularly distributed from the surface downwards with a tendency to avoid the actual surface layers.

Ratio, oblique hauls with ring-trawl : bottom plankton net=1 : 1.

CEPOLIDÆ.

Cepola rubescens L. (Red Band Fish).

Four post-larvæ of this species were taken on July 26th, two of 4½ mm. from 18·5 metres, and one each of 4½ and 5 mm. from 28·7 and 35·1 metres respectively. One of 3½ mm. was taken at the surface on August 4th.

CALLIONYMIDÆ.

Callionymus spp. (Dragonets).

Figure 4 shows the results of the collections of Callionymus post-larvæ in 1926; in the earlier months these will all be *C. lyra* (L.), but a few *C. maculatus* (Rafin.) will occur in the later collections. They confirm the previous conclusions that their region of maximum abundance lies below 20 metres. At the same time there is here definite evidence that in April and perhaps May the post-larvæ tend on the

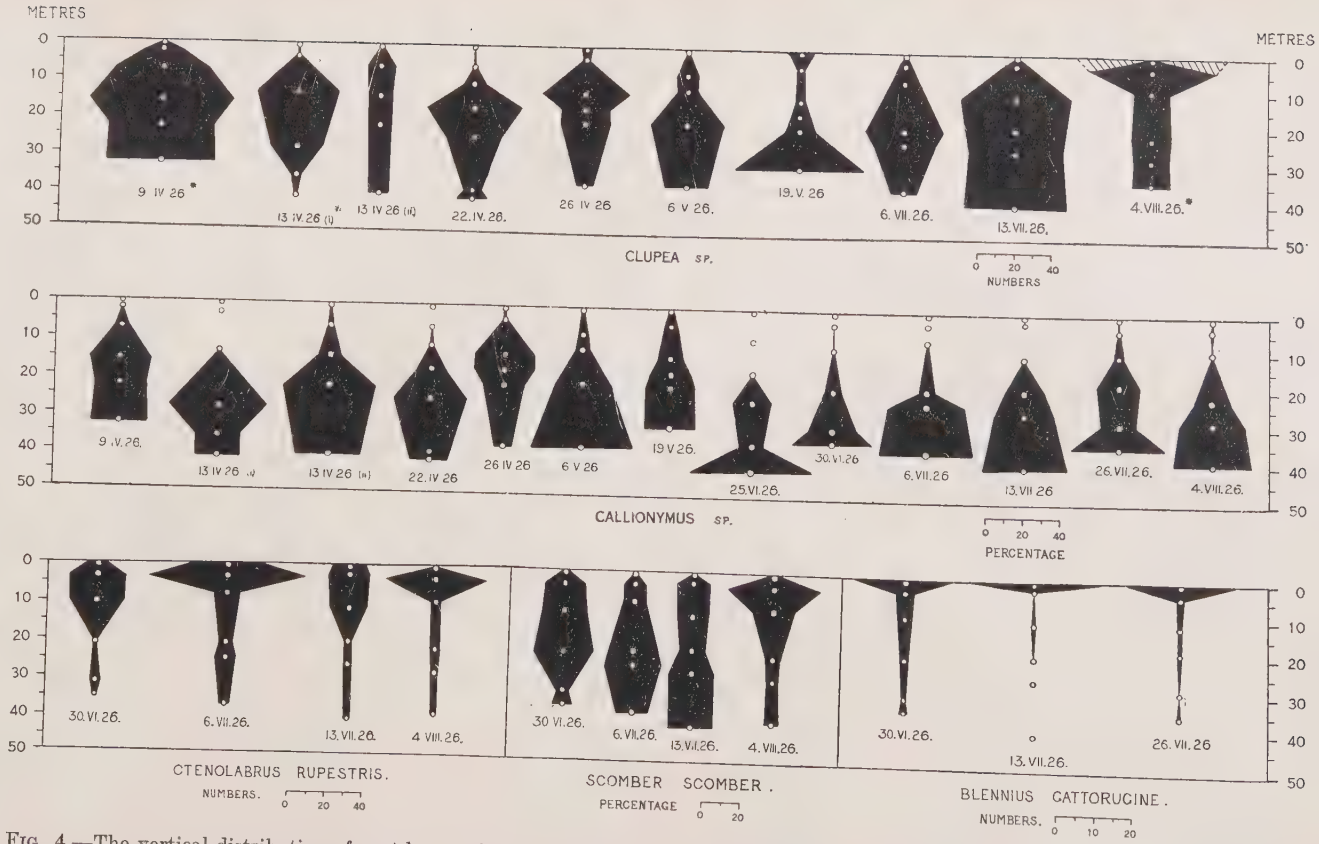

FIG. 4.—The vertical distribution of post-larvæ of the above species on the dates given. The white spots and black circles indicate the "average depths" at which hauls were taken. * Clupeid sp., on 9. iv. 26; 13. iv. 26 (i); and 4. viii. 26, are drawn to half the scale of the others.

whole to be higher in the water than in June, July, and August, because their numbers were still increasing with depth in the catches in these latter months, while in April the collections indicated that the region of maximum abundance had been fished through and their numbers were decreasing in the deepest hauls. See also Figure 2, p. 644, in which is given the average distribution in sunny weather as a result of superimposing all the records for April and May, and also those of June, July, and August.

Ratio, oblique hauls with ring-trawl : bottom plankton net=2·6 : 1.

LABRIDÆ (Wrasses).

The post-larvæ of five species of wrasse appear in these collections : *Labrus bergylta* Asc., *Labrus mixtus* (L.), *Crenilabrus melops* (L.), *Ctenolabrus rupestris* (L.), and *Centrolabrus exoletus* (L.). It was concluded in 1925 (**1**, p. 130) that " all species showed a tendency to be most abundant above 20–25 metres."

Although in 1926 *Ctenolabrus rupestris* was the only species present in any numbers, the following figures for the remaining species bear this out.

	Total numbers of post-larval wrasses caught.			
	Surface–10 m.	10–20 m.	20–30 m.	30–45 m.
Labrus bergylta	36	32	23	23
Labrus mixtus	9	8	20	20
Crenilabrus melops	24	12	4	3
Centrolabrus exoletus	15	5	6	3

Of these *Labrus mixtus* would appear to be the exception, although they are not definitely absent from the upper layers ; the few caught in the previous collections pointed to the majority being above 25 metres.

A figure showing the vertical distribution of *L. bergylta* post-larvæ has already been published (**3**, p. 846), when it was evident that the majority were at 10 metres or above.

As for the post-larvæ of *Ctenolabrus rupestris*, 4–8 mm. in length, the diagrams shown in Figure 4 and the numbers represented in the catches in Tables 3 and 4 show conclusively that this form definitely prefers the upper layers, and is indeed most abundant above 10 metres and at the surface itself.

The ratios, oblique hauls with ring-trawl : bottom plankton net were :— *L. bergylta* 1·4 : 1 ; *L. mixtus* 1·2 : 1 ; *C. melops* 0·4 : 1 ; *C. rupestris* 1 : 1 ; and *C. exoletus* 3·7 : 1.

TRACHINIDÆ.

Trachinus vipera C. and V. (Lesser Weever).

Post-larvæ of this species, 4–7 mm. in length, were only numerous in the catches on August 4th (Fig. 5, p. 662). On this occasion it was very

evident that, while they may be found at all depths, the post-larvæ showed a decided preference for the surface layers. This supports the indications given by the previous collections that they were most abundant above 25 metres.

Ratio, oblique hauls with ring-trawl : bottom plankton net=3 : 1.

SCOMBRIDÆ.

Scomber scomber (L.), (Mackerel).

In 1925 (**1**, p. 133) the indications were that post-larval mackerel were most numerous above 25 metres. Post-larvæ of this species, mostly 4–10 mm. in length, were unusually abundant in 1926, and Figure 4 and Tables 3 and 4 show that we have quite definite evidence as to their vertical distribution. We see that they tended to be very evenly distributed from the surface downwards, though there was a tendency for the numbers to be slightly less actually at the surface itself.

Actually the greatest catches on each day were on June 30th at 21·4 metres, on July 6th at 24·7 metres, on July 13th at 26·4 metres, on July 15th at E1 at 2·9 metres, on July 26th at 18·5 metres, and on August 4th at 3·5 metres. This indicates that while they may occur in numbers at any depth, there is perhaps a tendency for them to be most abundant round about 20–25 metres.

I give below the sizes of the mackerel post-larvæ caught at each depth on two occasions showing that there is no differentiation of size with depth.

July 6th, 1926	Length in millimetres. 4	5	6	7	8	9	10	11
Surface	–	3	1	1	1	–	–	–
3·3 metres	20		18	12	9	7	2	–
7·8 ,,	16	12	29	8	3	2	1	1
20·9 ,,	6	69	54	25	4	3	–	–
24·7 ,,	9	22	90	45	14	2	–	–
37·2 ,,	5	27	52	15	4	1	–	–

August 4th, 1926	Length in millimetres. 4	5	6	7	8	9	10	11	12	13	14
Surface (i)	–	2	1	4	7	7	1	–	1	–	–
,, (ii)	–	–	3	3	4	9	1	1	3	–	–
3·5 metres	1	5	21	25	40	32	15	3	2	–	–
9·5 ,,	1	8	13	14	16	7	3	–	–	1	1
22·2 ,,	–	1	7	5	4	4	1	1	–	–	–
28·2 ,,	–	–	8	5	3	1	–	1	–		–
39·4 ,,	–	4	8	4	3	2	–	–	–	–	–

Ratio, oblique hauls with ring-trawl : bottom plankton net=7·3 : 1.

ZEIDÆ.

Zeus faber L. (John Dory).

Only four post-larvæ of this species were taken ; one of $4\frac{1}{2}$ mm. at E1 from 13·7 metres on July 15th, and one of 5 mm. from 9·5 metres and two of 4 and $4\frac{1}{2}$ mm. from 28·2 metres on August 4th.

GOBIIDÆ (Gobies).

On occasions when post-larval gobies were at all numerous they were always taken from below about 25 metres (Fig. 5). This agrees with the results for the year 1925, but in the few collections made in 1924 they appeared to be higher in the water. It was remarked previously (**1**, p. 108) that by comparison with the numbers taken in 1924 there was an amazing absence of young gobies in 1925. During the course of a series of hauls taken during 24 hours on June 3rd–4th in 1926 however, the numbers of post-larval gobies show a great increase at night, there being more than eight times as many caught in the dark as in the daytime. In 1925, also from observations made two nights in succession (**2**, p. 398), it appears that the post-larval gobies were very much more abundant at night than in the daytime. This at once suggests that actually, although not present in the catches from the upper layers as abundantly as in 1924, they were not really scarce, but were living in the daytime in layers deeper than those sampled by the net in 1925 and 1926. Evidence obtained by means of the bottom plankton net gives a striking confirmation to this suggestion. Actually throughout the year on an average the bottom plankton net caught 298 times as many post-larval gobies as the oblique hauls with the ring-trawl. The greatest number of post-larval gobies were taken in July when the average half-hourly catch ($\times 8{\cdot}5$) with the bottom plankton net was 3247 as against 2·1 for the same time with the ring-trawl hauled obliquely through the upper water layers. This would seem to afford definite proof that normally in the daytime, at any rate in 1925, 1926, and 1927, the post-larval gobies, 4–12 mm. in length (species unidentified), live in the water layers immediately adjacent to the bottom. What was the cause for the unusual behaviour in 1924 when the post-larvæ were high in the water is not known, but there is evidence that other plankton animals behaved differently that year from the two succeeding years.

Ratio, oblique hauls with ring-trawl : bottom plankton net = 1 : 297·8.

Lebetus scorpioides (Coll.).

Post-larvæ of this species were never abundant, but as in previous records there was a tendency for them to keep to the deeper layers.

Actually 20 were caught between the surface and 10 metres, 7 between 10 and 20 metres, 49 between 20 and 30 metres, and 52 between 30 and 45 metres. They were most abundant on August 4th, and Table 4 definitely shows that they were most numerous below 20 metres and that their numbers were still increasing with depth.

Ratio, oblique hauls with ring-trawl : bottom plankton net=3·3 : 1.

BLENNIIDÆ (Blennies).

The three species of blennies whose post-larvæ appeared in the 1926 catches were *B. ocellaris* (L.), *B. pholis* (L.), and *B. gattorugine* (L.).

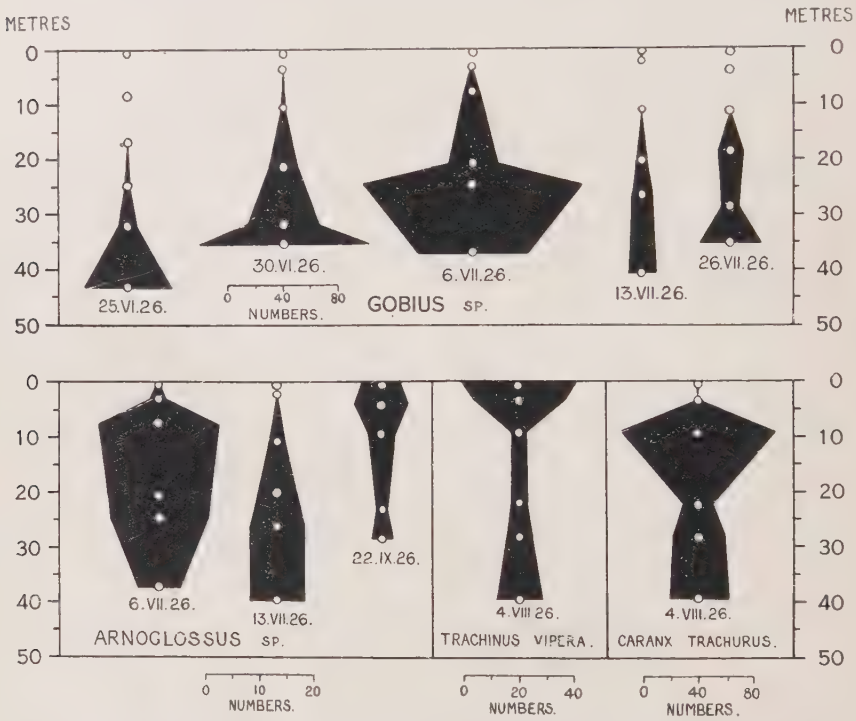

FIG. 5.—The vertical distribution of post-larvæ of the above species on the dates given. The white spots and black circles indicate the "average depths" at which hauls were taken.

Although few were taken in previous years the conclusions were (**1**, p. 135), "it would appear that on the whole the majority of the post-larvæ of the above three species frequented the water layers above a depth of 25 metres right up to the surface itself."

In 1926 the only species whose post-larvæ appeared in significant numbers was *Blennius gattorugine*, and Figure 4, p. 658, shows very clearly

that post-larvæ of this form, 5–10 mm. in length, definitely prefer the actual surface layers.

Ratio, oblique hauls with ring-trawl : bottom plankton net = *B. pholis* 0·6 : 1 ; *B. gattorugine* 0·7 : 1.

Chirolophis galerita L. (Yarrell's Blenny).

Four post-larvæ of this species occurred in the catches of 1925 (**1**, p. 154) on April 2nd and April 8th, but their presence was not mentioned in the text. These four specimens, 4–5 mm. in length, came from 5 metres, 12·5 metres (2), and 32·5 metres. In 1926 none were caught during the observations made on vertical distribution.

Ratio, oblique hauls with ring-trawl : bottom plankton net = 2·2 : 1.

Centronotus gunnellus Bl. Schn. (Gunnell).

Two post-larvæ of this species, 12 and 18 mm. in length, were caught from 22·4 metres on April 9th, 1926.

TRIGLIDÆ (Gurnards).

Post-larval gurnards, probably comprising *Trigla gurnardus* L. *T. cuculus* L., *T. hirundo* Bl., and *T. lineata* L., were not very numerous in the 1926 collections, but the few present tend to confirm the previous conclusions that post-larvæ, mostly 5–11 mm. in length, generally begin to become abundant at about 15 metres.

Ratio, oblique hauls with ring-trawl : bottom plankton net = 2·5 : 1.

COTTIDÆ.

Cottus bubalis (Euphr.), (Bullhead).

Only 17 post-larvæ of this species occurred in the 1926 collections, and of these 12 were caught from below 20 metres, which confirms the results of the few caught in the previous years.

Ratio, oblique hauls with ring-trawl : bottom plankton net = 6·7 : 1.

CYCLOPTERIDÆ.

Liparis montagui (Donov.), (Montagu's Sucker).

Only three post-larvæ of this species were taken, one from 21·6 metres, one from 39 metres, and one from 41 metres (Table 1.). Previous evidence, though slight, pointed to this being a deep-living form.

Only four were taken in the bottom plankton net.

GOBIESOCIDÆ.

Lepadogaster bimaculatus (Penn.), (Doubly spotted Sucker).

Twenty-four post-larvæ of this species were taken and of these 11 were caught between 20 and 30 metres, and 13 between 30 and 45 metres. This confirms the previous indications, and results with the bottom plankton net point to their living very near the bottom, as do also the 24-hour series on June 3rd–4th, 1926, when the post-larvæ showed a definite increase in numbers at night.

Ratio, oblique hauls with ring-trawl : bottom plankton net = 1 : 76·8.

LOPHIIDÆ.

Lophius piscatorius (L.), (Angler).

Eighteen post-larval anglers, 5–9½ mm. in length, were taken in 1926, and of these 2 occurred between the surface and 10 metres, 2 between 10 and 20 metres, 7 between 20 and 30 metres, 4 between 30 and 40 metres, and 3 below 40 metres.

SUMMARY.

1. From April to September in 1926 a further series of collections were made with the 2-metre ring-trawl in water 54 metres deep off Plymouth, to supplement the results already published (**1**) on the vertical distribution of post-larvæ of teleostean fishes in the daylight.

2. From June, 1927, to May, 1928, collections were made with a bottom plankton net for comparison with catches made with oblique hauls with the ring-trawl during the same period.

3. The results confirm to a very large extent the conclusions already published as to the vertical distribution of the post-larvæ of many of our commoner fish ; and the bottom plankton net collections together with the series of 24-hour observations already published (**2** and **3**), throw further light on the behaviour of such species as *Gadus minutus* and the Gobies.

4. The true distribution of the post-larvæ of the clupeids, the sprat and the pilchard, in the daytime remains yet to be discovered.

5. On page 642 is given a scheme in which the fish are classified as to their vertical distribution on a sunny day as far as is possible from the data obtained.

6. It is remarked that there is a definite difference in the behaviour of the post-larvæ of certain spring-spawning fish as opposed to those of summer-spawners. Most of the post-larvæ of spring-spawners keep to the layers below about 15 metres, while most of the latter are to be found above 25 metres up to the very surface itself.

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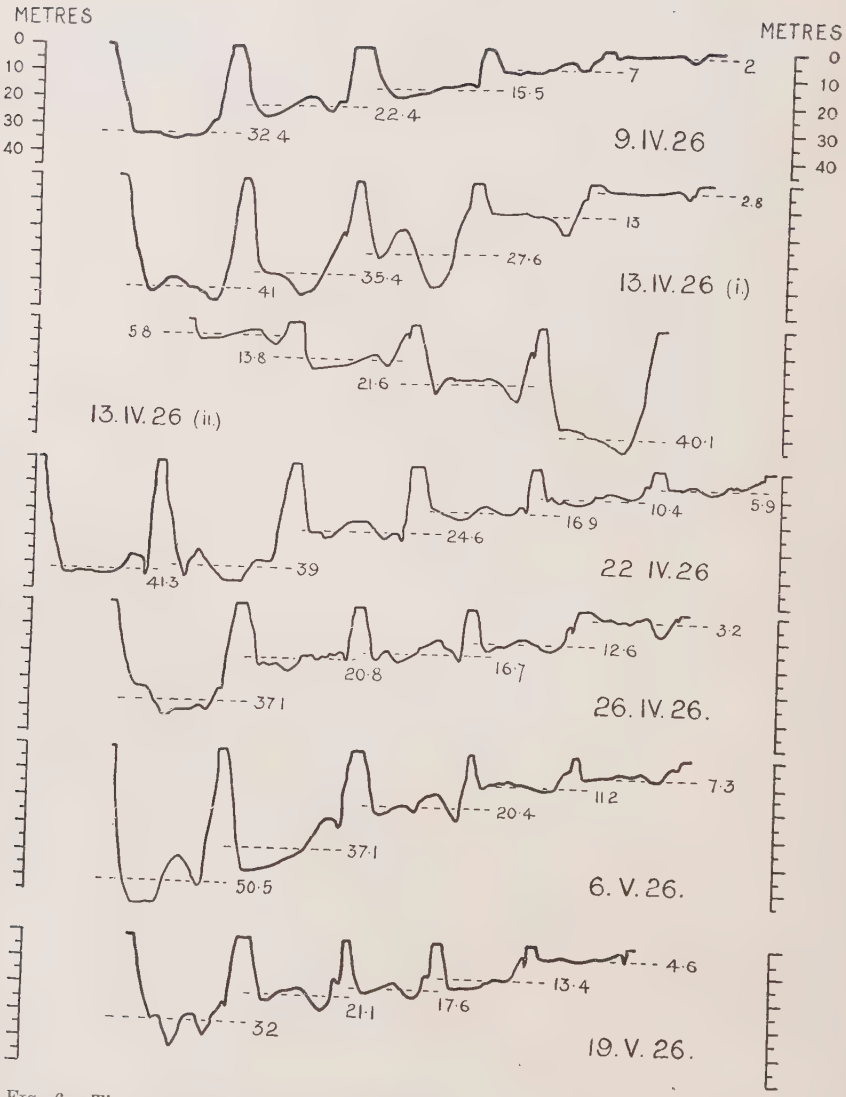

FIG. 6.—The series of curves given by the depth-recorder indicating the path of the net through the water for each haul on the dates given. The net enters the water on the right-hand side of each curve. The dotted lines indicate the calculated "average depth."

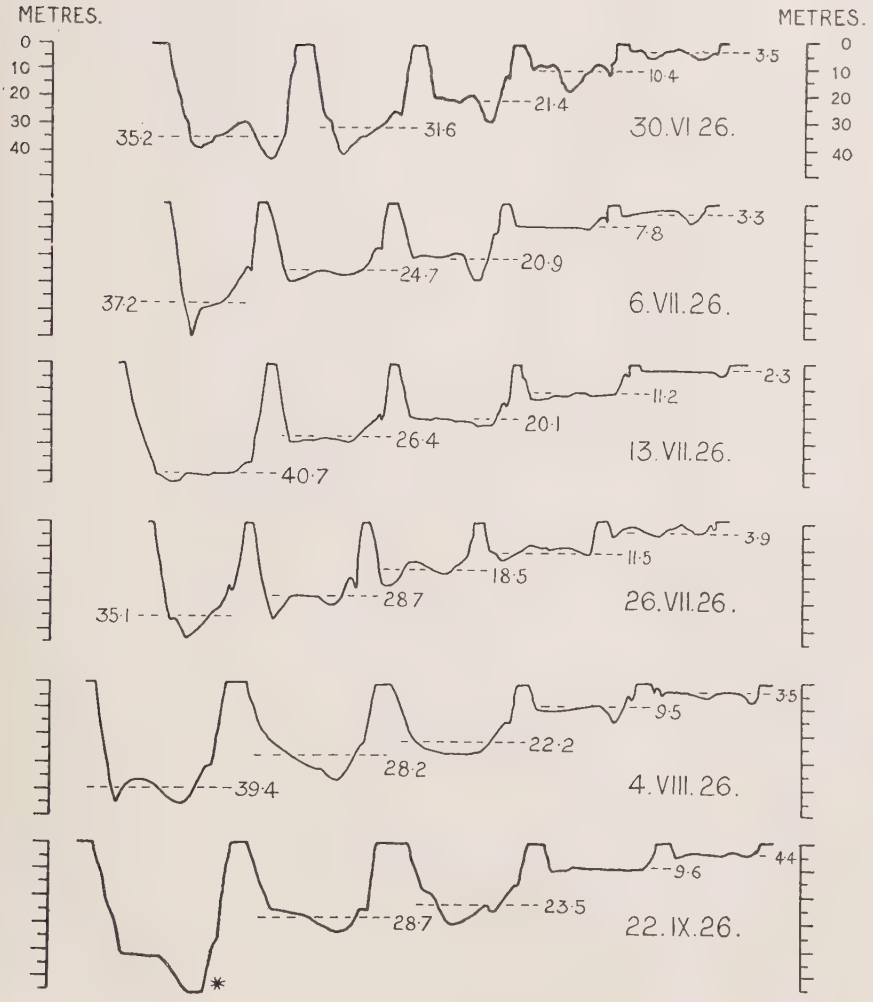

FIG. 7.—The series of curves given by the depth-recorder indicating the path of the net through the water for each haul on the dates given. The net enters the water on the right-hand side of each curve. The dotted lines indicate the calculated "average depth." * 22. ix. 26: Struck bottom.

List of Stations, 1926.*

Date.	Position.	Time.	Fishing depths in metres. Average.	Limits.	Remarks.
April 9th	A	11.29 a.m.	Surface	–	Bright sunshine; cloudless, except on horizon, which was hazy. Sea calm; but surface not smooth; slight swell. Wind light, from west.
		11.46 ,,	2	1·5–4	
		12.3 p.m.	7	4–9	
		12.22 ,,	15·5	12·5–18·5	Secchi disc 11.27 a.m. 10 m.
		12.42 ,,	22·4	18–25·5	1.25 p.m. 12 m.
		1.04 ,,	32·4	27–34	
April 13th (i)	A	11.3 a.m.	Surface	–	Bright sunshine; cloudless; slight haze. Sea flat calm; surface smooth without ripples. No wind. Like this all day.
		11.21 ,,	2·8	2·5–4	
		11·39 ,,	13	11–18	Secchi disc 11.00 a.m. 12 m.
		11.59 ,,	27·6	18–38	12.55 p.m. 10 m.
		12.18 p.m.	35·4	25–42	
		12.38 ,,	41	37·5–46	
April 13th (ii)	A	2.51 p.m.	Surface	–	(See above.)
		2.35 ,,	5·8	3·5–7·5	
		2.17 ,	13·8	10–16·5	
		1.58 ,,	21·6	19–27	
		1.40 ,,	40·1	36·5–45	
April 22nd	A	10.18 a.m.	Surface	0–3	Bright sunshine 8.30–10.00 a.m.; with cumulus. At 10.15 sky cloudless for considerable distance round sun, with a little high cirro-stratus: horizon cloudy. 11.10 a.m. sun clouded over: 11.59 a.m. sun shining. Sea surface calm but broken.
		10.35 ,,	5·9	3–8	
		10.56 ,,	10·4	6–13	
		11.15 ,,	16·9	15–19·5	
		11.35 ,,	24·6	21–27·5	Secchi disc 11.12 a.m. 10 m.
		11.59 ,,	39	35–45	1.40 ,, 11 m.
		12.22 p.m.	41·3	35–44	
April 26th	A	10.3 a.m.	Surface	–	Dull with thickish cloud early in morning; sun trying to break through later; sun shone at 10.40 a.m., but was soon covered again, showing only dimly for rest of hauls. Sea surface choppy; stiff N.W. breeze.
		10.21 ,,	3·2	1–8	
		10.38 ,,	12·6	7·5–16	
		10.52 ,,	16·7	11·5–20	
		11.12 ,,	20·8	18–25	Secchi disc 10.00 a.m. 11·5 m.
		11.35 ,,	37·1	31·5–40·5	12.45 p.m. 13 m.

May 6th	A	10.8 a.m.	Surface	–	Clear and cloudless until 10.00 a.m., when there was intermittent sunshine with cumulus clouds ; one or two drops of rain. Sea surface choppy ; stiff N.W. breeze.
		10.26 ,,	7·3	4–9	
		10·44 ,,	11·2	6·5–13	
		11.4 ,,	20·4	15–25	Secchi disc 10.7 a.m. 9·5 m.
		11.27 ,,	37·1	25–45	12.30 p.m. 9 m.
		11.48 ,,	50·5	40–58†	
May 19th	A	9.32 a.m.	Surface	–	Weather from sunrise to start of work close, sky overcast. Sun tried to come through at 10.00 a.m., but only shone brightly at last haul. Wind very slight ; sea surface with slight ripple.
		9.53 ,,	4·6	3–5	
		10.14 ,,	13·4	7–16·5	
		10.36 ,,	17·6	12·5–20	Secchi disc 9·25 a.m. 13 m.
		10·56 ,,	21·1	16–25	12.00 p.m. 11 m.
		11.22 ,,	32	25–40	
June 25th	A	9.52 a.m.	Surface	–	Cloudless ; slight haze ; no wind ; sea surface glass calm.
		10.10 ,,	8·2‡	6–9	Secchi disc 9.50 a.m. 19½ m.
		10·29 ,,	16·9‡	15–20	12.00 p.m. 20½ m.
		10.49 ,,	24·6‡	19–27	
		11·10 ,,	32‡	31–33	
		11.31 ,,	43·1‡	39–49§	
June 30th	L4	10.57 a.m.	Surface	–	A little very high cirrus, otherwise cloudless. Bright sunshine ; slight haze. Stiff east wind ; sea moderate.
		11·13 ,,	3·6	2–5·5	
		11.30 ,,	10·4	7–16	
		11.46 ,,	21·4	18–28	
		12.4 p.m.	31·6	25–39	
		12.24 ,,	35·2	30–42·5	
July 6th	A	9.56 a.m.	Surface	–	Very thick clouds ; dull ; visibility fair. Sea calm, but surface broken by breeze.
		10.11 ,,	3·3	2–6	
		10.28 ,,	7·9	5–9	Secchi disc 11.47 a.m. 14 m.
		10.45 ,,	20·9	18–28	
		11.5 ,,	24·7	17–28·5	
		11.28 ,,	37·2	25–50·5	

* All hauls were of 10 minutes' duration, the time given being the start of the haul.

‡ Drum of depth-recorder not screwed home ; 4 metres have been added to recorded depth.

† Net struck bottom.

§ Wire broke ; net fished for 13½ minutes.

Date.	Position.	Time.	Fishing depths in metres. Average.	Limits.	Remarks.
July 13th	A	9.41 a.m.	Surface	–	Cloudless; brilliant sunshine; haze in distance. Fresh easterly wind; sea surface choppy. Secchi disc 11.30 a.m. 13 m.
		9.58 „	2·3	2–4	
		10.15 „	11·2	10–12	
		10.33 „	20·1	15–22	
		10.53 „	26·4	20–29	
		11.11 „	40·7	35·5–44	
July 15th	E1	10.46 a.m.	Surface	–	Sun partially obscured by hazy cloud; visibility poor. Secchi disc 10.35 a.m. 12 m. 1.30 p.m. 13 m.
		11.00 „	2·9	1·5–4·5	
		11.15 „	6·6	4–8·5	
		11.33 „	13·7	11·5–19	
		11.53 „	21·5	17–23·5	
		12.10 p.m.	34·1	29–40	
		12.31 „	49	44–57	
July 26th	A	10.16 a.m.	Surface	–	Very dull and overcast at start of day, with heavy clouds; 9.45 a.m. clouds broke up and sun came out bright; remained out till 11.15 a.m.; 11.40 a.m. raining. Sea surface calm, but rippled. Secchi disc 12.00 p.m. 12 m.
		10.32 „	3·9	2–6	
		10.49 „	11·5	10–14	
		11·6 „	18·5	14–24	
		11.22 „	28·7	23–35·5	
		11.41 „	35·1	25–43	
August 4th	A	9.41 a.m.	Surface	–	Bright sunshine; cloudless; no haze. Sea surface choppy; slight swell. Secchi disc 12.55 p.m. 9 m.
		10.00 „	3·5	2·5–6	
		10.18 „	9·5	7–13	
		10.37 „	22·2	14·5–25	
		10.56 „	28·2	21–35	
		11.17 „	39·4	31·5–43	
		11.36 „	Surface	–	
September 22nd	A	1.20 p.m.	Surface	–	Weather dull; at 1.40 p.m. sun was shining through thin cloud for short time. Sea calm.
		1.40 „	4·4	2–5	
		1.57 „	9·6	9–10	
		2.18 „	23·5	15·5–30	
		2.39 „	28·7	25–33·5	
		2.58 „ ‖			

‖ Net struck bottom.

TABLE 1.

	Depth in metres.	Clupea sp.	Gadus pollachius.	G. merlangus.	G. minutus.	G. luscus.	G. callarias.	Onos sp.	Scophthalmus norvegicus.	Zeugopterus punctatus.	Pleuronectes limanda.	P. microcephalus.	P. flesus.	Solea vulgaris.	S. variegata.	Rhombus sp.	Ammodytes tobianus.	A. lanceolatus.	Callionymus sp.	Labrus bergylta.	Gobius sp.	Centronotus gunnellus	Trigla sp.	Cottus bubalis.	Liparis montagui.	Lophius piscatorius.	*Total Young Fish.*
April 9th, 1926	*S.*	–	1	–	–	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7
	2	39	5	2	–	–	1	17	–	–	–	–	1	–	–	–	2	–	1	–	1	–	–	–	–	69
	7	101	1	6	–	1	3	14	–	–	3	–	2	–	–	–	–	1	12	–	–	–	1	3	–	–	148
	15·5	151	2	52	6	–	8	15	–	–	4	2	5	2	–	–	2	4	50	–	–	–	5	1	–	–	309
	22·4	112	–	64	19	4	–	11	–	–	12	1	–	1	–	1	–	–	41	–	–	2	14	1	–	–	283
	32·4	117	–	55	22	3	1	15	–	–	13	1	2	6	–	–	1	1	46	–	1	–	1	4	–	–	289
April 13th, 1926 (i)	*S.*	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
	2·8	2	2	–	–	–	–	6	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	1	13
	13	87	4	4	1	–	–	24	–	–	10	6	–	–	–	1	2	–	–	–	–	–	1	–	–	–	140
	27·6	55	3	54	17	2	1	10	–	–	25	1	1	2	–	–	3	–	33	–	1	–	9	–	–	–	217
	35·4	11	–	25	13	1	1	4	–	–	4	–	2	1	–	–	–	–	15	–	–	–	2	–	–	–	79
	41	2	1	3	5	–	1	3	–	–	5	–	3	–	–	–	–	–	15	–	–	–	–	1	1	–	40
April 13th, 1926 (ii)	*S.*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	5·8	15	1	9	–	–	–	7	–	–	1	–	3	–	–	–	1	2	2	–	–	–	–	–	–	–	41
	13·8	13	–	18	2	–	1	12	–	–	2	–	2	–	–	–	1	2	7	–	2	–	2	–	–	–	64
	21·6	13	1	56	11	1	2	7	–	1	17	–	7	2	–	–	–	–	29	–	1	–	5	–	1	–	154
	40·1	11	1	9	3	–	2	2	–	1	4	–	3	1	–	–	5	–	20	–	–	–	2	1	–	–	65
April 22nd, 1926	*S.*	1	1	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6
	5·9	2	–	2	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	5
	10·4	12	3	2	2	1	–	1	–	–	5	–	10	1	–	–	–	1	8	–	–	–	2	–	–	–	48
	16·9	51	–	45	31	3	–	1	1	1	41	4	8	8	12	–	–	2	77	–	3	–	5	–	–	–	293
	24·6	30	1	51	132	13	–	3	1	4	49	6	7	11	20	–	1	–	186	2	3	–	6	1	–	–	527
	39	10	–	21	144	5	–	3	2	–	10	2	2	10	5	–	1	–	110	–	2	–	–	–	1	1	329
	41·3	17	4	13	131	6	–	–	2	–	11	3	1	18	5	–	1	2	95	–	6	–	1	3	–	–	319

TABLE 2.

	Depth in metres.	Clupea sp.	Gadus pollachius.	G. merlangus.	G. minutus.	G. luscus.	Molva molva.	Onos sp.	Raniceps raninus.	Scophthalmus norvegicus.	Zeugopterus punctatus.	Pleuronectes limanda.	P. microcephalus.	P. flesus.	Solea vulgaris.	S. variegata.	Rhombus sp.	Ammodytes tobianus.	A. lanceolatus.	Callionymus sp.	Labrus bergylta.	Labrus mixtus.	Crenilabrus melops.	Ctenolabrus rupestris.	Centrolabrus exoletus.	Scomber scomber.	Gobius sp.	Lebetus scorpioides.	Blennius pholis.	B. gattorugine.	Trigla sp.	Lepadogaster bimaculatus.	*Total Young Fish.*
April 26th, 1926	*S.*	6	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7
	3·2	4	–	–	–	–	–	1	–	–	–	6	–	–	–	7	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	17
	12·6	47	–	12	13	1	–	–	–	1	1	11	6	–	–	7	–	–	100	–	–	–	–	–	–	–	–	–	–	–	–	199
	16·7	16	–	1	22	–	1	1	–	1	1	6	2	–	–	2	–	–	98	–	–	–	–	–	–	–	–	–	–	–	–	153
	20·8	27	–	21	25	2	–	–	–	1	–	7	2	–	1	12	–	–	68	–	–	–	–	–	–	1	–	–	–	1	–	169
	37·1	9	2	2	23	–	–	–	–	–	–	9	2	–	1	1	–	–	33	–	–	–	–	–	–	–	–	–	–	2	–	84
May 6th, 1926	*S.*	–	2	1	–	–	–	25	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	29
	7·3	12	5	1	–	–	–	12	–	1	–	1	–	–	–	–	–	–	11	1	–	–	–	–	–	–	–	–	–	–	–	46
	11·2	11	2	–	–	–	–	3	–	1	–	2	5	–	–	–	1	1	15	1	–	–	–	–	–	–	–	–	–	–	–	43
	20·4	39	4	56	–	–	–	18	–	2	–	46	22	2	–	–	–	–	54	1	–	–	–	–	–	–	–	–	–	1	–	246
	37·1	23	2	13	30	6	1	13	–	1	2	34	3	–	1	12	–	–	98	–	–	–	–	–	–	–	–	–	–	1	–	244
May 19th, 1926	*S.*	13	1	10	–	–	–	3	–	–	–	–	1	–	1	5	–	–	24	1	–	–	–	–	–	–	–	–	–	–	–	59
	4·6	4	–	25	–	–	–	3	–	2	–	–	–	–	–	6	–	–	132	3	–	–	–	–	–	–	–	–	–	3	–	181
	13·4	5	1	14	10	2	1	–	–	12	–	12	2	–	–	11	–	–	267	3	–	–	–	–	–	–	–	–	–	1	–	348
	17·6	11	1	24	12	–	7	1	–	10	2	12	6	–	–	43	–	–	401	–	1	–	–	–	–	–	–	–	–	5	–	549
	21·1	26	–	35	16	3	–	1	–	14	–	13	21	–	2	46	–	–	498	1	1	–	–	–	–	–	–	1	–	7	1	696
	32	70	1	30	87	2	10	1	–	17	6	64	44	–	3	74	–	–	493	–	–	–	–	–	–	–	–	2	–	4	–	921
June 25th, 1926	*S.*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	2	–	–	4
	8·2	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	8	1	8	1	3	1	–	–	2	3	–	–	28
	16·9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	2	–	3	–	–	1	1	–	1	2	–	–	13
	24·6	2	–	3	–	–	–	–	–	3	–	–	3	–	–	–	–	1	3	41	4	–	3	–	–	2	5	2	–	4	1	–	77
	32	–	–	–	–	–		–	–	4	–	–	–	–	–	–	–	–	4	26	1	1	2	–	–	–	14	–	1	–	1	–	54
	43·1	–	–	–	–	–	–	–	1	9	–	2	1	–	–	2	–	–	2	127	1	2	1	–	–	1	64	3	–	–	1	2	219

TABLE 3.

	Depth in metres.	Clupea sp.	Gadus merlangus.	Onos sp.	Merluccius merluccius.	Ranieeps ranimus.	Capros aper.	Arnoglossus sp.	Scophthalmus norvegicus.	Pleuronectes microcephalus.	Solea variegata.	S. lascaris.	Rhombus sp.	Serranus cabrilla.	Caranx trachurus.	Ammodytes lanceolatus.	Callionymus sp.	Labrus bergylta.	L. mixtus.	Crenilabrus melops.	Ctenolabrus rupestris.	Centrolabrus exoletus.	Trachinus vipera.	Scomber scomber.	Zeus faber.	Gobius sp.	Lebetus scorpioides.	Blennius ocellaris.	B. pholis.	B. gattorugine.	Trigla sp.	Lepadogaster bimaculatus.	Lophius piscatorius.	*Total Young Fish.*
June 30th, 1926	*S.*	1	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10	–	–	7	–	–	–	–	–	26	–	–	–	**46**
	3·5	6	–	1	–	–	–	–	–	–	–	–	1	–	–	1	–	8	–	8	31	2	–	31	–	–	–	–	1	5	–	–	–	**95**
	10·4	6	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	1	–	7	29	4	–	35	–	2	–	–	–	4	–	–	1	**92**
	21·4	8	3	1	–	–	–	1	7	5	5	–	–	–	–	3	26	4	3	1	1	3	1	47	–	22	–	–	3	2	2	–	1	**149**
	31·6	6	1	2	–	–	–	4	5	4	–	–	–	–	–	6	74	7	1	–	5	2	3	10	–	54	5	–	1	1	2	1	–	**194**
	35·2	21	1	–	–	–	–	2	8	3	–	–	–	–	–	6	183	4	3	–	2	–	–	16	–	123	1	–	–	2	1	2	1	**379**
July 6th, 1926	*S.*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	37	2	–	6	–	–	–	–	–	–	–	–	–	**45**
	3·3	8	3	–	–	–	–	3	–	–	–	–	–	–	–	3	–	–	–	–	83	3	–	68	–	–	1	–	2	–	–	–	–	**174**
	7·8	16	–	–	–	–	–	22	–	–	–	–	7	–	–	1	–	–	–	–	14	3	1	72	–	12	5	–	2	–	–	–	–	**155**
	20·9	42	–	–	–	–	–	19	1	1	–	–	1	–	–	–	8	–	2	–	7	1	1	161	–	37	7	2	–	3	–	–	2	**295**
	24·7	33	–	–	–	–	–	18	4	3	2	–	–	–	1	9	40	1	1	–	11	–	–	182	–	159	2	–	1	–	5	1	–	**473**
	37·2	13	–	–	–	–	–	8	5	4	3	–	2	–	–	4	49	–	2	–	5	1	–	104	–	79	3	1	–	2	–	1	2	**288**
July 13th, 1926	*S.*	–	1	–	–	–	–	–	–	–	–	–	3	–	–	–	1	–	–	–	18	–	–	16	–	1	–	–	–	35	–	–	–	**75**
	2·3	16	–	–	–	–	–	–	–	–	–	–	2	–	–	6	–	–	–	–	22	–	4	77	–	–	–	–	1	–	–	–	–	**128**
	11·2	59	–	–	–	–	–	3	–	–	–	–	2	–	–	5	–	–	–	–	20	1	2	73	–	1	3	–	–	1	–	–	1	**171**
	20·1	54	–	–	–	–	–	7	–	–	4	1	–	–	1	6	14	–	–	–	4	1	4	61	–	7	4	1	–	–	1	–	1	**171**
	26·4	50	1	–	–	–	–	10	–	–	6	–	–	–	3	5	21	–	2	–	4	–	5	106	–	15	3	–	–	–	1	–	3	**235**
	40·7	54	–	–	1	2	–	10	–	–	4	–	–	–	–	20	30	–	1	–	3	–	2	99	–	21	6	–	–	–	3	1	1	**258**
July 15th, 1926	*S.*	4	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	2	–	1	14	–	–	–	–	–	–	–	–	–	**23**
	2·9	27	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	15	–	1	44	–	–	–	–	–	–	–	–	–	**90**
E 1	*6·6*	69	–	–	–	–	–	–	–	–	–	–	2	–	2	1			–	–	5	–	–	34	–	–	–	–	–	5	–	–	–	**118**
	13·7	255	–	–	–	–	1	6	–	–	–	–	4	1	4	1			–	–	3	–	7	23	1	2	–	1	–	–	–	–	–	**309**
	21·5	30	–	–	–	1	–	1	–	–	–	–		–	–	1	1		–	–	6	–	2	14	–	1	1	–	1	–	–	–	–	**59**
	34·1	254	–	–	–	1	–	13	–	1	–	–	–	–	–	2	31	–	–	–	1	–	–	31	–	13	1	1	3	–	–	–	–	**352**
	49	203	–	–	1	–	–	6	–	2	–	–	–	–	2	2	59		–	–	2	–	1	26	–	26	–	–	2	–	–	–	2	**334**

TABLE 4.

	Depth in metres.	Clupea sp.	Gadus merlangus.	G. luscus.	Merluccius merluccius.	Raniceps raninus.	Capros aper.	Arnoglossus sp.	Scophthalmus norvegicus.	Solea variegata.	Rhombus sp.	Serranus cabrilla.	Caranx trachurus.	Belone vulgaris.	Ammodytes lanceolatus.	A. tobianus.	Cepola rubescens.	Callionymus sp.	Crenilabrus melops.	Ctenolabrus rupestris.	Centrolabrus exoletus.	Trachinus vipera.	Scomber scomber.	Zeus faber.	Gobius sp.	Lebetus scorpioides.	Blennius ocellaris.	B. gattorugine.	Trigla sp.	Lepadogaster bimaculatus.	*Total Young Fish.*
July 26th, 1926	*S.*	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	1	–	–	–	4	–	–	–	–	29	–	–	**36**
	3·9	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	2	–	–	6	–	1	–	–	2	–	–	**16**
	11·5	4	–	–	–	–	–	1	–	–	1	–	–	–	2	–	4	–	1	–	1	11	–	–	–	–	1	1	–	**27**
	18·5	11	–	–	2	–	–	3	–	2	–	–	1	–	7	–	17	–	2	–	–	12	–	18	4	–	1	–	–	**82**
	28·7	6	–	–	1	–	–	1	–	1	–	–	–	–	4	–	14	–	1	1	3	5	–	13	2	–	–	3	–	**56**
	35·1	10	–	–	1	1	–	4	1	1	1	–	2	–	10	–	36	–	3	–	3	8	–	44	11	3	1	–	1	**142**
August 4th, 1926	*S.* (*i*)	7	–	–	–	–	–	1	–	–	3	–	–	–	–	–	2	–	–	–	42	23	–	1	1	–	–	2	–	**82**
	S. (*ii*)	163	–	–	–	–	–	2	–	–	4	–	8	1	6	–	7	–	54	1	19	24	–	8	–	–	48	–	–	**346**
	3·5	134	1	–	–	–	–	–	–	–	7	2	1	–	29	–	3	–	5	–	34	144	–	1	3	–	1	–	–	**365**
	9·5	39	–	–	–	–	–	–	–	–	4	–	111	–	6	–	–	–	5	–	5	64	1	–	8	–	9	1	–	**253**
	22·2	43	–	–	–	–	3	4	–	–	–	–	22	–	5	–	27	–	3	–	6	23	–	4	7	1	5	1	1	**155**
	28·2	37	–	1	–	–	–	3	–	–	–	–	38	–	3	–	50	–	3	–	10	18	2	3	15	–	2	1	2	**188**
	39·4	40	–	4	–	–	–	12	–	–	2	–	42	–	2	–	59	–	1	–	17	21	–	2	17	1	–	5	1	**226**
September 22nd, 1926	*S.*	–	–	–	–	–	–	7	–	–	–	–	8	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	**16**
	4·4	1	–	–	–	–	–	10	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	2	–	–	–	–	**15**
	9·6	1	–	–	–	–	–	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	**7**
	23·5	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	**2**
	28·7	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	**5**

Table 5.

Average Monthly Catches of Bottom Plankton Net, 30-minute Hauls Multiplied by 8·5.

	1928					1927							
	Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Total.
Clupeid sp.	35·7	50·2	51·0	65·5	74·0	0·9	7·7	6·0	6·8	13·6	17·0	6·0	334·4
Gadus pollachius	–	–	–	0·9	–	–	–	–	–	–	–	–	0·9
G. merlangus	–	0·9	0·9	9·4	2·5	–	–	–	–	–	–	–	13·7
G. minutus	–	–	146·2	1047·7	1680·5	7·7	–	–	–	–	–	–	2742·1
G. luscus.	–	0·9	1·7	6·0	12·8	–	0·9	1·7	–	1·7	11·1	8·5	45·3
Onos sp.	–	–	–	2·6	4·3	2·6	0·9	–	–	–	–	–	10·4
Merluccius merluccius	–	–	–	–	–	–	–	–	1·7	–	–	–	1·7
Arnoglossus sp.	–	–	–	–	–	0·9	3·4	5·1	2·6	–	–	–	12·0
Scophthalmus norvegicus	–	–	–	1·7	10·2	2·6	0·9	–	–	–	–	–	15·4
Zeugopterus punctatus	–	–	–	0·9	1·7	–	–	–	–	–	–	–	2·6
Pleuronectes limanda	–	–	0·9	15·3	23·0	7·7	–	–	–	–	–	–	46·9
P. flesus	–	.	–	2·6	–	–	–	–	–	–	–	–	2·6
P. microcephalus	–	–	1·7	7·7	11·1	–	–	–	–	–	–	–	20·5
Solea vulgaris	–	–	8·5	4·3	4·3	–	–	–	–	–	–		17·1
S. variegata	–	–	–	–	12·8	–	–	–	–	–	.	.	12·8
S. lutea.	–	–	–	–	–	0·9	–	–	–	–	.		0·9
Ammodytes tobianus	0·9	68·0	1·7	0·9	1·7	–	–	–	–	–	–	–	73·2
A. lanceolatus	–	11·1	1·7	11·1	–	0·9	11·9	–	–	–	–	.	36·7
Callionymus sp.	–	–	6·0	44·2	150·5	22·1	17·0	4·3	3·4	3·4	–	–	250·9
Labrus bergylta	–	–	–	–	–	6·0	–	–	–	–	–	–	6·0
L. mixtus	–	–	.	–	–	0·9	–	–	–	–	–	–	0·9
Ctenolabrus rupestris	–	–	–	–	–	5·1	6·0	–	–	.	–	–	11·1
Crenilabrus melops	–	–	–	–	–	5·1	0·9	–	–	–	–	–	6·0
Centrolabrus exoletus	–	–	–	–	–	–	0·9	–	–	–	–	–	0·9
Scomber scomber	–	–	–	–	–	2·6	0·9	–	–	–	–	–	3·5
Gobius sp.	3·4	1·7	5·1	4·3	114·8	1354·1	3247·0	109·7	59·7	11·1	6·0	26·4	4943·3
Crystallogobius nillsoni	–	–	–	41·7	95·2	34·0	30·6	1·7	0·9	–	–	–	204·1
Lebetus scorpioides	–	–	–	–	–	–	0·9	–	0·9	–	–	–	1·8
Trachinus vipera	–	–	–	–	–	–	0·9	1·7	–	–	–	–	2·6
Blennius pholis	–	–	–	–	–	2·6	–	–	–	–	–	–	2·6
B. gattorugine	–	–	–	–	–	–	9·4	–	–	–	–	–	9·4
Chirolophis galerita	–	0·9	–	.	–	–	–	–	–	–	–	–	0·9
Trigla sp.	–	–	–	.	8·5	–	0·9	0·9	–	–	–	–	10·3
Cottus bubalis	–	–	1·7	–	–	–	–	–	–	–	–	–	1·7
Lepadogaster bimaculatus	–	–	–	–	14·5	5·1	9·4	1·7	–	–	–	–	30·7

Table 6.

Average Monthly Catches in Ring-Trawl, 30-minute Oblique Hauls.

	1928					1927							
	Jan.	Feb.	March.	April.	May.*	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Total.
Clupeid sp.	23·7	30·3	11·1	82·5	*25·0*	8·1	81·3	14·1	1·2	2·4	30·0	22·5	332·2
Gadus pollachius	–	–	1·2	21·6	*1·6*	–	–	–	–	–	–	–	24·4
G. merlangus	–	–	7·8	29·7	*55·9*	8·4	0·6	0·2	–	–	–	–	102·6
G. minutus	–	3·9	24·6	135·6	*33·6*	–	–	–	–	–	–	–	197·7
G. luscus.	0·9	6·9	5·4	8·4	*1·8*	0·3	0·3	0·6	0·3	2·1	3·9	49·5	80·4
Onos sp.	–	–	–	31·8	*10·4*	0·9	–	–	–	–	–	–	43·1
Merluccius merluccius	–	–	–	–	–	–	0·2	0·6	–	1·5	0·9	–	3·2
Arnoglossus sp.	–	–	–	–	–	–	15·0	7·2	3·0	0·9	–	–	26·1
Scophthalmus norvegicus	–	–	–	4·8	*29·8*	3·6	0·9	–	–	–	–	–	39·1
Zeugopterus punctatus	–	–	0·7	2·1	*6·2*	–	–	–	–	–	–	–	9·0
Pleuronectes limanda	–	–	6·6	37·2	*45·3*	2·1	–	–	–	–	–	–	91·2
P. flesus	–	–	0·3	10·8	*0·7*	–	–	–	–	–	–	–	11·8
P. microcephalus	–	–	0·3	17·7	*16·1*	0·6	–	–	–	–	–	–	34·7
Solea vulgaris	–	–	0·3	3·3	*1·0*	–	–	–	–	–	–	–	4·6
S. variegata	–	–	–	10·3	*40·5*	0·3	–	–	–	–	–	–	51·1
S. lutea.	–	–	–	–	–	0·3	3·6	–	–	–	–	–	3·9
Ammodytes tobianus	0·6	90·9	20·7	0·9	*0·1*	0·3	–	–	–	–	–	–	113·5
A. lanceolatus	–	–	–	21·0	*13·9*	5·4	3·6	0·9	–	–	–	–	44·8
Callionymus sp.	–	–	8·7	212·1	*377·6*	24·1	11·4	7·8	1·8	18·9	0·9	–	663·5
Labrus bergylta	–	–	–	–	*1·3*	6·9	–	–	–	–	–	–	8·2
L. mixtus	–	–	–	–	*0·2*	0·9	–	–	–	–	–	–	1·1
Ctenolabrus rupestris	–	–	–	–	–	0·6	6·0	4·5	–	–	–	–	11·1
Crenilabrus melops	–	–	–	–	–	2·4	–	–	–	–	–	–	2·4
Centrolabrus exoletus	–	–	–	–	–	3·0	0·3	–	–	–	–	–	3·3
Scomber scomber	–	–	–	–	*0·1*	1·2	23·4	0·9	–	–	–	–	25·6
Gobius sp.	–	–	–	2·1	*1·8*	2·1	2·1	6·1	0·9	0·6	0·9	–	16·6
Crystallogobius nillsoni	–	–											–
Lebetus scorpioides	–	–	–	–	*0·2*	0·3	1·2	1·5	0·3	0·3	–	2·1	5·9
Trachinus vipera	–	–	–	–	–	1·2	2·4	3·9	0·3	–	–	–	7·8
Blennius pholis	–	–	–	–	*0·1*	0·3	0·9	0·3	–	–	–	–	1·6
B. gattorugine	–	–	–	–	–	0·9	2·1	3·6	–	–	–	–	6·6
Chirolophis galerita	–	–	2·0	–	–	–	–	–	–	–	–	–	2·0
Trigla sp.	–	–	1·5	0·3	*13·4*	3·9	6·0	1·5	–	–	–	–	26·4
Cottus bubalis	–	–	4·7	6·0	*0·7*	–	–	–	–	–	–	–	11·4
Lepadogaster bimaculatus	–	–	–	–	*0·1*	–	–	0·3	–	–	–	–	0·4

* The figures given here are the average catches per half-hour haul obtained from the years 1924, 1925, 1926, 1927, and 1929, the total number of hauls at each station being regarded as one oblique haul in the first three years.

Bottom Fauna and the Food of Fishes.

By

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With 1 Chart and 3 Figures in the Text.

In the waters off Plymouth there exists a definite inshore fishing-ground, approximately 13 square miles in area, locally known as the "corner." In order to obtain some idea of the Bionomic conditions prevailing on this ground an intensive study of the bottom fauna was undertaken. Quantitative seasonal observations extending over a period of one year (August, 1928–July, 1929 inclusive) have been made, using the 0·1 square metre Bottom Sampler and the "Agassiz" Trawl, a method having been devised for obtaining quantitative hauls with the latter instrument. Investigations into the food actually eaten by the fishes within the area have been carried on simultaneously, and the stomach contents of over 2000 fishes comprising 29 different species have been examined. On account of the length of time required for stomach examination, it was found impossible to make seasonal observations on them also, but comparable winter and summer examinations were made.

I am deeply indebted to Dr. Allen and the Staff of the Laboratory for much advice and other assistance throughout the course of this work. My very best thanks are also due to Capt. Lord and the crew of the s.s. *Salpa* for their invaluable co-operation and constant endeavour to reap the best results from all operations at sea.

Methods of Collection.

The quantitative faunistic observations were made in the first place by means of the Petersen 0·1 square metre bottom sampler (Petersen "grab"). Fifteen stations were fixed, more or less evenly distributed over the area—i.e. one station to rather less than one square mile (see Chart, p. 678). In autumn, 1928, and in winter, spring, and summer following, five bottom sampler hauls were taken at each of these stations.

Examination of the stomach contents of fishes from the same area soon disclosed the fact that a number of organisms—Pandalidæ, Crangonidæ,

Palæmonidæ, Hippolytidæ—were being preyed upon which were not represented at all in grab samples. A species of Portunus—*P. depurator* also appeared frequently in stomach contents but not in grab hauls. An additional quantitative collecting method had therefore to be devised to supplement that of the bottom sampler. For this purpose the " Agassiz " trawl was eventually used in the following manner.

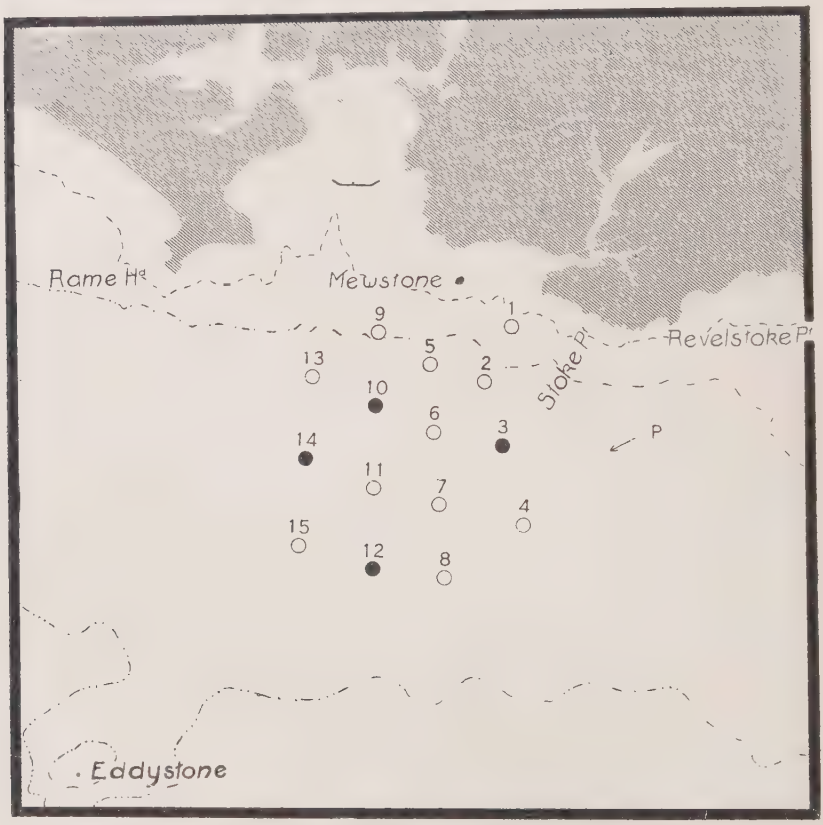

Chart of Bottom Sampler Stations and Trawl Centres on the " Corner " Fishing Ground off Plymouth, 1928–29.

o = Bottom Sampler Stations.
● = Bottom Sampler Stations also used as Trawl Centres.

Four representative grab stations—3, 10, 12, 14—were chosen as trawling centres. A trawler's " dan " was anchored on the station to be worked. The trawl was then shot so as to strike bottom as nearly as possible alongside the dan and towed in a straight line away from it for a distance of approximately 520 yards. Four hauls were taken around each trawl centre, towing in directions north, south, east, and west in turn from

the dan. The distance trawled was ascertained by using a range-finder* for observing the distance of the ship from the dan when the trawl was hauled clear of the bottom, due allowance being made for the length of warp paid out. The trawl used had a 7-foot beam—i.e. the mouth was 7 foot wide. By towing it over a distance of 520 yards, therefore, an area of approximately $\frac{1}{4}$ acre was covered at each haul. Thus a total area of roughly one acre was represented by the four trawl samples taken around each trawl centre. Unfortunately the trawl and range-finder were not brought into operation while the first (autumn) series of grab samples was being taken, so that trawl records are available only for the winter, spring, and summer seasons (Table IV).

By the use of the range-finder and dan one at least of the objections put forward by Petersen (**19**, p. 47) against the use of the trawl for quantitative estimation of the animal life on the sea bottom is overcome. He says, "If we wish to have accurate information regarding the amount of animal life, especially the number of individuals per unit of surface, we must rely upon other apparatus than the dredge and trawl; with these it is difficult to say what distance they have been dragged over the bottom, nor can we know how many animals they have left behind on the distance worked over: the number is often many times that taken up." The latter objection still holds. But even though it be impossible to estimate how many animals a trawl fails to capture, it is nevertheless permissible to hold the view that the animals it does bring up represent, at any rate, the minimum number of individuals present on the area covered. And this is all that can be claimed for the bottom sampler. It may and probably does bring up samples which represent fairly accurately the population of a sea bottom composed of soft mud or mire such as seems to be typical of much of the Limfjord (**19**, p. 14), for example. But on bottoms of a harder nature composed of sand or gravel, either with or without an admixture of mud, the performance of the bottom sampler is not so satisfactory. We can count the number of individuals it brings up, but have no way of knowing how many animals it leaves behind in their burrows beyond the reach of its "bite." Moreover, in such places as the Limfjord, active members of an epifauna, such as *Portunus depurator* which abounds on the "corner" grounds off Plymouth, appear to be present only in negligible numbers. Where such occur they too, more often than not, evade capture by the grab, probably scuttling out of its way as it descends upon them from above. Such species as *Pandalina brevirostris*, Palæmonidæ, and the Crangonidæ, important food animals in the "corner" area, do not come within its scope at all:† the trawl, whatever its limitations, is the most effective instrument for their capture. In order, therefore, to

* The instrument used was a Barr and Stroud range-finder, type F.T. 32. Base 80 cm.

† It is not designed to capture these animals.

acquire more complete data regarding the food animals present upon the ground under investigation than was possible with the bottom sampler alone, both sampler and trawl have been used in conjunction, the former for bringing up the sedentary infauna and the latter for the more active animals roaming on or above the sea bottom.

THE BOTTOM FAUNA.

In Table III is recorded the number of individuals of separate species or homogeneous groups per 0·5 square metre at each station as brought up in 5 hauls of the 0·1 square metre bottom sampler. Columns a, b, c, d are the data for autumn, 1928, and the following winter, spring, and summer respectively. Table IV records the number of animals brought up by the "Agassiz" trawl from $\frac{1}{4}$ acre of bottom N., S., E., and W. of each of the four stations 3, 10, 12, and 14. Only three seasons' observations (b, c, d) are available as explained above.

Seasonal observations were taken in order to determine what fluctuations, if any, of density or distribution of the bottom invertebrates take place in the course of a year. It will be seen from the tables that on the whole, both number and distribution of most of the organisms remained fairly constant. *Pandalina brevirostris* and some Crangonids were the only species which showed very definite migratory movements (Table IV). During the winter months Pandalina was more or less evenly distributed over the whole of the "corner" ground in depths of from 25–28 fathoms, with a tendency to be most numerous near the south-western edge where the water is deepest. In spring, Pandalina had moved shorewards and congregated in an immense shoal along the outer edge of the rough ground between Stoke Pt. and Revelstoke Pt. (see chart). They had then all but disappeared from most of the "corner" area west of stations 3 and 4, but were very numerous at those points and south-eastwards of them. A $\frac{1}{4}$-acre "Agassiz" haul taken in the month of April, towing from the point P on the chart in the direction indicated by the arrow, contained 537 individuals.

This shoreward migration in the spring seems to be a spawning migration into shallower water. In March, ovigerous females carrying eggs of a very pale pink colour became numerous in the catches. As the eggs ripen their colour changes to pale green, when they are ready to be shed. "Green-bellied" females became numerous in May and remained plentiful until the end of July. The main spawning season, therefore, seems to extend over a period of about three months. A certain amount of spawning evidently goes on for a longer time for the larvæ were abundant in the plankton until September and a few were still to be found at the time of writing (October, 1929).

Kemp (**12**) and Murie (**17**) describe a similar gregarious migratory habit in another Pandalid, *Pandalus montagui*. But in the case of this species the spawning migration is an off-shore one. Murie (p. 245) states that although nothing definite is known on this point, yet there is good reason for believing that around the long parallel sand-banks girding the outer arch facing Essex, the " pink shrimps " of the Thames estuary flock in the early spring to spawn. And the Humber shrimp trawlers " know quite well that the appearance of ' green-bellies ' is a sign that the prawns will soon be off to sea " (**12**, p. 88, footnote). It may be, then, that in estuarine regions such as those of the Thames and Humber, the large sand-banks and sand-flats at their mouths far off-shore, provide for *P. montagui* conditions suitable for spawning similar to those sought by *Pandalina brevirostris* in an in-shore migration from the deep and open sea.

Two species of the Amphipod genus Ampelisca—*A. spinipes* and *A. tenuicornis*—are present on the " corner " grounds. The former species is confined to bottoms of fairly clean sand or shell gravel—e.g. on and around Station 1. The latter with a preference for more muddy conditions is present over the whole area with the exception of Station 1. For convenience the two species are grouped together as Ampelisca spp. in Table III. From this table it will be seen that in autumn, 1928, these Amphipods were numerous on the western line of stations—13, 14, 15 and were also distributed in small numbers over the remainder of the area. In the following winter, however, they had almost entirely disappeared from the grounds, as recorded by the bottom sampler. Several additional hauls taken outside the area, both to seaward and to landward, also revealed a scarcity of Ampelisca. At first it was thought that, on the approach of winter, a great diminution in their numbers had taken place, either by natural death or otherwise. But this explanation had to be abandoned when young Rays (20–30 cm.) captured on the " corner " grounds at this time were found to have been feeding largely, and in some cases exclusively, on Ampelisca (Table II, p. 695). It is evident, therefore, that the Amphipods were still abundantly available to the fishes on the ground although, for some reason, the grab failed to capture them. Unfavourable weather and bad working conditions when the winter hauls were taken, which may suggest itself as a possible explanation, does not apply. Winter stations 13, 14, and 15 were worked in much more favourable conditions of wind and sea than were encountered at stations 9, 10, 11, and 12, for example, in the spring series of observations when 42, 109, 35, and 9 individuals respectively were taken off 0·5 square metres. Possibly Ampelisca may burrow deeply into the mud during the winter months, beyond the reach of the grab. In any case, whatever the explanation, the facts are interesting and important in so far as they serve to

illustrate the danger of assuming that a species is absent from the grounds when it is not to be found in the bottom sampler hauls.*

Perusal of Tables III and IV serves to show the great (numerical) richness of the organisms comprising the infauna as compared with those of the epifauna, even allowing for any discrepancy there may be in the sampling efficiency of the grab and trawl. The numbers as a whole, in both tables, are roughly of the same order of magnitude. But, where they represent the population of 0·5 square metre in the case of the grab samples (Table III) they represent the population of $\frac{1}{4}$ acre ($=0{\cdot}5$ sq. m. $\times 2023{\cdot}35$) for trawl samples (Table IV). Of *Upogebia deltaura*, for example, a burrowing crustacean found all over the "corner" grounds, totals of 11, 5, 14, and 18 individuals were taken at all stations in autumn, winter, spring, and summer respectively. These numbers captured over an area of $15 \times 0{\cdot}5$ square metres represent a calculated population of 1484, 674, 1888, 2428 individuals respectively per $\frac{1}{4}$ acre. For *U. stellata* the corresponding figures, as calculated, are 674, 674, 1349, and 1484 respectively. These numbers are far in excess of those for any species of the epifauna.

From Table III it will further be seen that the two species of Upogebia, considered together, are fairly uniformly distributed over the whole area. Calculating further on this basis, the Upogebia spp. population of the "corner" grounds exceeded 72 millions, 45 millions, 108 millions, and 130 millions in the autumn, winter, spring, and summer seasons respectively. These values, large though they be, probably fall far short of the actual numbers present, as, owing to the burrowing habit of this animal and the agility with which it darts into and along its underground passages, the bottom sampler is not likely to capture more than a small fraction of the total number of individuals present in the area from which it "bites."

The two species of Upogebia, therefore, form in themselves alone a vast potential food supply on the "corner" grounds. Nevertheless, although present in far greater numbers than *Portunus depurator*, for example, it does not necessarily follow that they are actually more important as a source of fish food. Prey, to be of service to any animal, must first of all be caught and eaten.

On this point, Ford (**7**, p. 532) remarks, "Before the potential value of a bed of Lamellibranchs as food for fishes can become known, the precise food value of the successive stages of the life-history of each lamellibranch must be determined. One species may never grow beyond a size which a medium-sized Dab could easily swallow whole, whereas another although it may be easily devoured in its early life will soon grow

* In this connexion, the relative inefficiency of every type of gear when compared with fishes as collectors, may be cited. In the waters off Plymouth, Sipunculus has never been taken in any collecting instrument. Nevertheless, this Gephyrean is commonly found in the stomachs of Rough Dogfishes (*Scyliorhinus canicula*) caught in these waters.

to a size quite beyond the largest of shell-eating fish and thus be relatively useless to fishes. In quantitative estimations of fish food similar to those made by the Danish investigators, this fact needs careful consideration." With sedentary hard-shelled organisms such as Lamellibranchs, size is the main consideration. But the burrowing habit of Upogebia and the alacrity with which it can scurry to safety, make its relatively great elusiveness as compared with that of Portunus, for example, a significant factor which must be taken into consideration in any attempt to estimate their relative values as sources of fish food.

This factor—*the comparative availability of the food animals present on or in the sea-floor*—is one the importance of which impresses itself upon the investigator, but except in certain cases—e.g. effect of size—he remains powerless to grapple effectively with it.* The availability of any animal for food, leaving out consideration of size, will depend upon :

1. The habits and activity of the organism itself ;
2. The habits and activity of the fish.

This will vary :

1. For the same organism with different fishes ; and
2. For different organisms with the same fish.

This variation of habit also affects grab samples, although it is impossible here also to obtain data by means of which its magnitude can be estimated and allowed for. A grab sample, in the opinion of the writer, must not be taken as a true or even approximate measure of the absolute numbers of animals present upon the sea bottom. In the Plymouth waters, at any rate, it is a *differential sample of the organisms*, ranging from 100 per cent (e.g. small Lamellibranchs and Gastropods, *Echinocyamus pusillus*, *Ophiothrix fragilis*) downwards (e.g. Upogebia, tubicolous Polychætes, *Portunus depurator*), according to their several abilities to elude the sampler. When considering grab results, this must always be borne in mind. In view of these facts, to work out the rough weights and dry weights of the organisms captured in the bottom sampler on the " corner " grounds, and to deduce therefrom the total amounts of the different types of food available over the area did not seem to be justified.

FOOD AND FEEDING HABITS OF FISHES.

General.

Examination of the stomach contents of fishes actually caught upon the grounds investigated by grab and trawl revealed that Ogilvie's statement with regard to post-larval herrings holds good in a general way

* See also **19**, p. 67, lines 7–10.

for all fishes—i.e. "within limits determined by size and suitability in other respects, the fish will eat what they can get" (**18**, p. 10). This fact is clearly demonstrated by examining fishes from grounds on which different bottom-dwelling animals predominate. For example, *Portunus depurator* is common on the "corner" grounds, while *Corystes cassivelaunus* and *Atelecyclus septemdentatus* are rarely found. But farther out in the direction of the Eddystone, Corystes and Atelecyclus, though not numerous, are fairly common and *P. depurator* less abundant. This change of fauna is reflected in the food of *Gadus luscus*, *Raia clavata*, and *Scyliorhinus canicula* trawled from those two areas (Table I).*

TABLE I.

Difference in Food of *Gadus luscus*, *Raia clavata*, and *Scyliorhinus canicula* on "Corner" and Outside Grounds.

		Stomachs containing *Portunus depurator*		Stomachs containing Corystes and/or Atelecyclus		Total number of stomachs examined
		Number	%	Number	%	
Gadus luscus	Corner	60	**36·8**	4	2·5	163
	Outside	19	25·7	16	**21·6**	74
Raia clavata	Corner	65	**38·9**	9	5·4	167
	Outside	12	24·5	18	**36·7**	49
Scyliorhinus canicula	Corner	18	11·8	1	0·7	152
	Outside	7	11·3	13	**21·0**	62

When, therefore, the food of the entire fish population of any particular area is considered as a whole, the organisms most commonly eaten are (with certain exceptions such as Echinodermata and Cœlenterata) found to be those most numerous and/or easily available. This does not apply, of course, to every species of fish considered individually, because for one reason or another some fishes are "selective" feeders: i.e. they are fitted by structure or habit to catch and eat certain animals and not others, when they are said to "select" the former and "reject" the latter.

A noteworthy feature of the "corner" grounds at the present time is the great scarcity of all kinds of Flatfishes except *Pleuronectes microcephalus* (the Lemon Dab) and *Arnoglossus laterna* (Scaldback). Only very occasionally are Sole, Brill, Turbot, and Flounder taken in the trawl, and Dab and Plaice are almost equally scarce. The absence of the last-named fish may be due to a corresponding paucity in the Lamellibranch, and in fact, the entire Molluscan fauna within the area. Although quantitative records are lacking, there is little doubt that during a

* See also **2**, p. 46, par. 3.

number of years immediately following the War *Aequipecten opercularis* (Queens)* at any rate was abundant. Plaice were then also numerous.

There is some indication that Queens are again on the increase. Should they once more populate the area it will be interesting and instructive to observe whether or not Plaice also return in numbers to the grounds.

The Lemon Dab (*Pleuronectes microcephalus*), though not abundant, is fairly numerous.† This may possibly be due to the fact that its diet consists mainly of Polychæta, the numbers of which probably have remained undiminished in spite of intensive trawling over the area.

The Scaldback (*Arnoglossus laterna*) -unfortunately not a marketable fish—is very plentiful. This again is probably to be explained by the presence of an abundant supply of suitable food organisms—Amphipoda, Schizopoda, Crangonidæ, Pandalidæ, and *Crystallogobius nilssonii*.

Periodic Change of Food.

As would be expected from the constancy of the constitution of the invertebrate fauna throughout the year, there is little obvious change of food in the summer and winter seasons. Nevertheless, there is, in certain cases at least, a definite *periodic* change. The Whiting, for example, normally feeds on a wide range of animals, its diet including large and small Crustaceans of all kinds, Worms and small Fishes (including the young of its own species), and an occasional Mollusc and Echinoderm. But Whiting of all sizes from 10 cm. in length upwards, caught in May and June, 1929, were found to be feeding almost exclusively on the Megalopa larvæ of *Corystes cassivelaunus*. Of fishes between 10 and 15 cm., twenty-five were examined. Two of those had their stomachs empty : all the others had been feeding on the larvæ. Of fishes over 15 cm. in length, fifty specimens were examined, forty-seven of which had been feeding on the Megalopas, *thirty-three of them exclusively*. In many cases the stomachs of the fish were simply gorged with the larvæ, some counts recording over 200 individuals per stomach.

The Whiting, in Plymouth waters, is a migratory species. Small fish appear in numbers from about May onwards, the larger fish following later in the season. A few may remain in the neighbourhood throughout the year. The fact that the time of their reappearance in numbers in the Plymouth area this year coincided with the presence of immense shoals‡

* Local fishermen state that trawling for Queens on and to the eastward of this area yielded very large hauls of the bivalves. Now they are so scarce that a whole day's takings would fall far short of an hour's catch in those years.

† This fish also is not quite so plentiful as formerly.

‡ One of these shoals was encountered in a small boat at sea about noon on the 20th May, 1929. For several miles the Megalopas were so numerous near the surface that two or three at a time could be scooped up in an ordinary cocoa-tin. A striking feature of the shoal was that all the larvæ were swimming rapidly, and all in the same direction.

of Corystes Megalopas in these waters, and that when caught the Whiting were found to be feeding almost entirely on the larvæ, suggests the possibility that the fish may have been attracted by this abundance of food. This view cannot definitely be put forward, however, without further evidence gleaned over a number of years.

Nineteen Whiting between 5 and 10 cm. in length were captured. Of these, two had empty stomachs, and seventeen had been feeding on small fishes, mostly *Crystallogobius nilssonii*, but one (9 cm.) had taken a Mackerel Midge (Onos sp.). Only two had eaten Megalopas, the stomach of one containing two and the other three individuals. The reason why these very small Whiting had not been feeding on the larvæ, as had the larger sizes, is not apparent.

Correlation of Habit and Structure with Food Eaten.

The habits of fishes—as of all animals—are inextricably bound up with structure and structure with habit. How the one affects the other does not concern us here. But both are important factors, influencing to a great extent the type of animal upon which a fish will normally depend for food. Because of their intimate relationship, therefore, the parts played by these two factors in determining the staple food of different fishes will be considered together.

The prey which a fish can capture is dependent to a large degree upon its feeding habits or foraging methods. These differ markedly in different fishes, and there is found always to be a corresponding difference in the type of organisms which form their staple food. This can best be illustrated by studying closely certain fishes with very typical and contrasting methods of feeding.

The **Lemon Dab** (*Pleuronectes microcephalus*). On the "corner" grounds the Lemon Dab feeds exclusively upon Annelids. This is entirely in keeping with the habits of the fish. It is a frequenter of muddy bottoms where worms are abundant and other organisms correspondingly scarce. Tubicolous Polychætes, which form the bulk of the Annelid fauna, cannot be captured by lying in wait for them : they have to be hunted and that discreetly, otherwise they disappear to safety down their tubes. So the Lemon Dab, if observed in an aquarium tank, is found to be of a very restless disposition. It is constantly on the move, swimming for short distances with intervening halts for brief periods. It comes to rest in a characteristic attitude, with the head and forepart of the body raised well off the substratum. Remaining perfectly still in this position, the fish, by means of its very prominent and exceedingly movable eyes, scans the bottom in its immediate neighbourhood (Fig. 1). Should it then observe a food organism—i.e. the anterior end of a worm cautiously emerging

from its burrow—the Lemon Dab suddenly pounces upon it like a true hunter with a kind of forward leap, bringing its mouth down almost vertically upon its victim by a strong arching of the anterior part of the

FIG. 1.—The Lemon Dab, *Pleuronectes microcephalus*.
Top ..... great range of eye movement.
Bottom..... typical attitudes of the fish when lying in waitf or prey.
(After Brightwell.)

body (Fig. 2). Foraging thus, it is not surprising that Todd (**29**, p. 104), during his researches upon the food of fishes in the Southern North Sea, should have found that the Lemon Dabs of that area were feeding to a considerable extent upon a species of Cerianthus.

It is somewhat strange, however, that of all these fishes from the "corner" grounds which have been examined, not one contained the slightest trace of a Lamellibranch. This may possibly be due to the great scarcity of these Molluscs in this area. On the other hand, there is every indication that the Lemon Dab does not "bite" its food. The nipped-off ends of tubicolous Polychætes are seldom or never found in its stomach: the whole worm is withdrawn unbroken from its burrow or tube. This being so, large Lamellibranchs perhaps are powerful enough to pull their siphons out of the fish's mouth even if they are caught. Small ones may

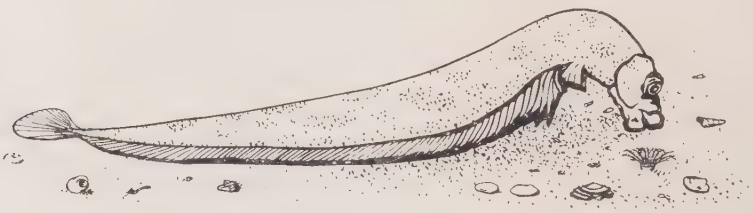

Fig. 2.—A Lemon Dab in the act of pouncing upon a tubicolous worm.

not be able to do so, but as the fish is not fitted for crushing hard shells, these are probably rejected when the valves are drawn into its mouth.

Ramsay Smith (**23**, p. 213) found that while Annelids formed the chief food of Lemon Dabs in the Firth of Forth, Hermit Crabs—*Eupagurus bernhardus* and *Anapagurus lævis*—also entered largely into their diet. In view of this statement, a number of small Hermits were introduced into aquarium tanks containing Lemon Dabs in order to observe what would happen. The fish immediately set about hunting the crabs in exactly the same manner as that described above for the capture of tubicolous Polychætes. With head raised well above the crab, the fish waits and watches until the Hermit ventures to appear at the mouth of its shell and then suddenly pounces upon it. Generally the crab shoots back to safety too quickly to be taken, as it usually walks about with only the tips of its walking legs and chelæ exposed. Moreover, the fish has to lie in wait facing the mouth of the shell, and the Hermits were frequently observed to dart back before emerging far enough even to crawl, having seen that danger threatened as soon as their eyes -conveniently placed on the tips of long eye-stalks—projected far enough to see up round the lip of the shell. The Lemon Dabs hunted more successfully, however, when a shell with its contained Hermit happened to be over-

turned. The crab is then obliged to expose much more of its body in its efforts to regain a normal position. In these circumstances, a fish was occasionally able to stalk and capture an unlucky Hermit. There seems then to be little doubt that small Pagurids would figure much more prominently in the diet of the Lemon Dab were it not for their extreme wariness and ability to beat a hasty retreat into the safety of their shells. On the " corner " grounds off Plymouth, the worm fauna appears to be large enough to support the Lemon Dabs of the area without their having to hunt such elusive prey. At any rate, small Hermits, though abundant, are not eaten.

The **Sole** (*Solea vulgaris*). The feeding habits of the ordinary Sole are very different from those of the Lemon Dab, and there is a corresponding difference in its diet. In foraging for prey the true Sole depends almost entirely on the tactile sense. The eyes, unlike those of the Lemon Dab which hunts by sight, are very small and scarcely movable. But the fish is provided with a dense mass of tactile villi on its lower cheek, which is thus equipped to function as a very sensitive tactile organ. When in search of food, the Sole creeps very slowly over the bottom using its lateral fins more for walking than for swimming, the fin spines in their motion resembling very much the legs of a centipede. As it moves along, the fish thoroughly explores the substratum by what may be described as a kind of patting and grubbing action of the snout, carefully feeling the objects in its path with the sensitive papillæ on its lower cheek. Bateson (**1**, p. 240) states that, so far as he could determine, the Sole is unable to find food which does not lie on the bottom, and will not succeed in finding food suspended in the water close above it unless it is lowered so that the fish is able to cover it with the lower surface of its head, when it is seized at once.

Unfortunately, *Solea vulgaris* was not obtainable in sufficient numbers from the " corner " to enable any definite conclusion to be drawn as to its staple food. But it may be significant that the few which were examined had been feeding on Eulalia, Phyllodoce, *Porcellana longicornis*, and Mollusca. Todd (**29**, p. 117), however, examined 212 stomachs containing recognisable food material. Of these, Polychæta were present in 59 per cent, Crustacea in 30 per cent, Pisces and Mollusca each in 11 per cent, Echinodermata in 9 per cent, Nemertinea in 3 per cent, and Polyzoa and Cœlenterata in less than 0·5 per cent. The principal food species were :—

Polychæta :	*Lagis koreni*, *Ophelia limacina*, Nephthys sp., and *Sabellaria spinulosa*.
Crustacea :	Ampelisca sp.
Mollusca :	*Scrobicularia* (=*Syndosmya*) *alba*.
Pisces :	*Pleuronectes limanda* (1·9–2·8 cm.), Ammodytes sp.
Echinoderms :	*Echinocyamus pusillus*.

It will at once be seen that all the above animals are such that a Sole, foraging for food in the manner described, might be expected to find and contrive to capture. The worms eaten, for example, are either free-living forms which creep over the sea bottom or, if tubicolous, are sluggish and vulnerable species such as the Pectinaridæ which inhabit shallow and friable tubes.

It has not been found possible to study the feeding habits of the other species of Sole, but it is probable that they all adopt essentially the same methods, all having sensitive papillæ developed to a greater or less extent on the lower cheek.

Besides the structural differences already mentioned, the Lemon Dab and Sole exhibit still other morphological modifications correlated with their modes of feeding. The Lemon Dab has a very small terminal mouth, with teeth on both sides, but best developed on the lower side. In the Sole, on the other hand, the mouth is not terminal, but curved down ventrally, and teeth are present only on the lower side. The Lemon Dab depends entirely upon the visual sense in foraging for its prey and is therefore a day feeder. The Sole is almost, if not quite, independent of vision for the finding and recognition of its food, and feeds mostly at night.

Dab and **Plaice** (*Pleuronectes limanda* and *P. platessa*). Both are visual feeders. The former forages in a manner similar to that of the Lemon Dab, but does not raise itself quite so far off the bottom or bring its mouth down upon its prey at such a steep angle. It shoots upon them more from a horizontal direction, and being an active and alert fish it is thus able to capture a greater range of organisms than the Lemon Dab, but is less successful when it comes to Polychætes alone. The hunting posture of the Plaice is still more nearly horizontal, the head being raised off the bottom even less than that of the Dab. Its food is therefore again more restricted in its range, approaching that of the Sole—i.e. Mollusca, errantiate Polychætes, and sometimes a few Crustaceans, including an occasional Upogebia.

Among Flatfishes, the direct effect of structure in determining the kind of food which is eaten is also clearly seen in the post-larval stages, which do not come within the scope of this work. Lebour (**13**, p. 443), however, has shown that young Pleuronectids fall into two groups according to the structure of the alimentary canal. One group includes *Solea vulgaris*, *S. variegata*, *S. lascaris*, *Pleuronectes limanda*, *Rhombus maximus*, *R. lævis*, *Zeugopterus punctatus*, *Z. unimaculatus*, and *Scophthalmus norvegicus*, each of which possesses a large mouth and short thick gullet and stomach. Very soon after hatching these fishes all feed upon small Copepoda and Cladocera. The second group includes *Pleuronectes flesus*, *P. microcephalus*, and *Arnoglossus laterna*, which have a small mouth and

long narrow gullet and stomach. These do not eat Copepods or any other Crustacea until a greater size is reached, subsisting at first largely on a vegetarian (Diatom) diet, and going on to Entomostraca only at a much later stage.

The **Gurnards.** Definite correlation between the habits of a fish and its staple food organisms is also well seen in the case of the Gurnards. Four species—*Trigla lineata*, *T. cuculus*, *T. gurnardus*, *T. hirundo*—are present in small numbers in the Plymouth area. If these four species be observed in aquarium tanks, they will be found to form a definite habitudinal series. *T. lineata* spends most of its time crawling over the bottom of the tank by means of its long finger-like pectoral filaments. In addition to their locomotor function, the filaments are also very efficient tactile organs used in the finding and identification of food. As the fish creeps slowly over the bottom, the filaments are kept in continuous motion thoroughly "fingering" the ground over which they pass. When anything which promises to be suitable as an article of diet is touched by one of the filaments, the fish suddenly wheels round upon it and either immediately swallows it, or subjects it to still further tactile "scrutiny." *T. cuculus*, *T. gurnardus*, and *T. hirundo* also possess pectoral filaments and use them in the manner described, but to a progressively less extent. These species depend more and more upon the visual sense for the recognition of their prey, and dart upon it from a distance. Thus we find that *T. lineata* feeds very largely upon *Porcellana longicornis*, and to a less extent upon Galathea, *Portunus pusillus*, and Amphipoda. Burrowing organisms such as Upogebia and those tubicolous Polychætes which retract with almost lightning-like rapidity on the slightest provocation do not figure in its diet any more than do such active swimmers as the Pandalidæ, Crangonidæ, Palæmonidæ, or Pisces. But those agile organisms which successfully elude capture by *T. lineata* fall easy victims to the three other species which are more active hunters, depending less upon the tactile than upon the visual sense in foraging for their prey.

The **Dragonet** (*Callionymus lyra*). *Callionymus lyra*, too, is an interesting feeder whose habits are clearly reflected in its diet. This fish, a bottom dweller, is continually in a state of restless activity, in this somewhat resembling the Lemon Dab. For a few moments it will remain still, the anterior part of its body raised slightly off the ground as the fish rests poised upon its large pectoral fins. Then it skims along for a short distance, swimming usually less than a centimetre off the bottom, and again comes to rest. In this way Callionymus explores thoroughly a large and representative area of the sea floor, and few organisms escape its attention. Its food, therefore, is varied in the extreme. Ophiuroids, small Echinoids such as *Echinocyamus pusillus* and the young of larger species,

all the bottom-living Crustacea of suitable size—e.g. Amphipoda, Schizopoda, Porcellana, Galathea, Upogebia (occasionally), Paguridæ, *Portunus pusillus*, Ebalia, Inachidæ—small Mollusca of every description, and errantiate Polychæta are all to be found in the stomachs of Callionymus. Tubicolous Polychætes appear generally to elude it. Palæmonid, Crangonid, and Pandalid Crustaceans, too, it seldom captures, perhaps because they are too alert, but more probably because they live as a rule just above the bottom in a plane which Callionymus does not frequent (see also p. 693).

Other Fishes. The feeding habits of the other fishes from the " corner " have not been studied in detail. Of such forms as the Gadoids little can be

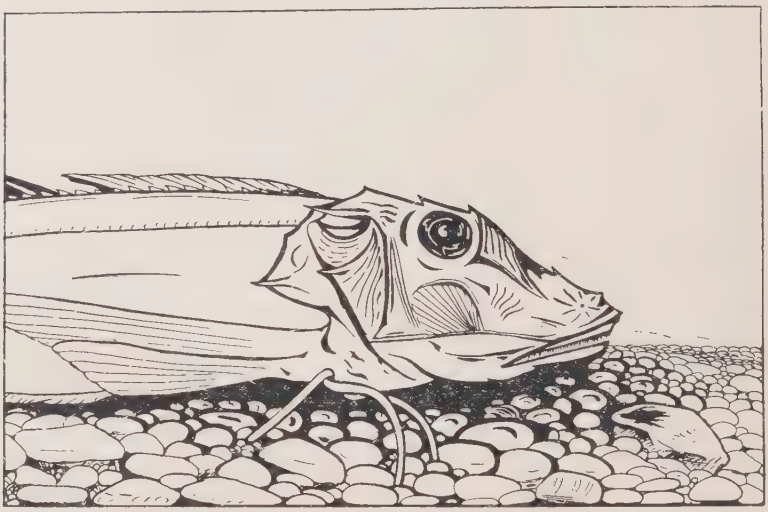

Fig. 3.—*Trigla hirundo* " feeling " its way along the sea floor by means of its long finger-like pectoral filaments.

added to what is already generally known. They are roving fishes which feed by sight, but some of them, such as the Pouting and Cod, appear to use their barbel as a tactile or gustatory organ. They will snap at almost anything which comes within their reach, whether on or off the bottom. Thus their food is almost as varied as the fauna of the area in which they are living. On the " corner " grounds only Whiting (*Gadus merlangus*), Whiting Pout (*G. luscus*), and the Poor-cod or Bib (*G. minutus*) are taken in any numbers. The first-named fish, while it feeds both on and off the bottom, confines its attention mostly to actively swimming pelagic organisms, while the two others graze more upon the bottom-dwelling animals (Table V).

Of the Dogfishes only two species have been taken during these

investigations. The feeding habits of these voracious members of the Shark tribe are also well known. The Rough Dogfish (*Scyliorhinus canicula*) feeds on anything which comes in its way. It hunts by scent, and although remaining for the most part in the lower layers also scours the sea from bottom to surface. The Spur Dog (*Squalus acanthias*), on the contrary, feeds while in Plymouth waters almost entirely on Herring. In fact it is present in numbers in the Plymouth area only during the winter months when Herrings are abundant. Todd (**29**, p. 132), however, states that in the North Sea its diet is much more comprehensive, including besides Pisces, Crustacea, Gephyrea, and often large quantities of *Pleurobrachia pileus*.

The four species of Ray examined feed almost entirely on the various Crustaceans available in their neighbourhood. Of their actual methods of feeding nothing has been seen.

Bionomics.

Elton (**6**, p. 59), in discussing food chains, states that they stop at certain points because there are very definite limits, both upper and lower, to the size of food an animal can eat. The size of the prey of carnivorous animals (both terrestrial and aquatic) is limited in the upward direction by their strength and ability to catch the prey, and in the downward direction by the feasibility of getting enough of the smaller organisms to satisfy their needs, the latter factor being also strongly influenced by the numbers as well as the size of the food animals. There is therefore an optimum size of food which is the one usually eaten. In the sea, however, another very important factor is involved which Elton does not mention possibly because it is very much less evident on the land. Animals of a suitable size for food, although living in the same area, may move in quite a different plane from that frequented by the carnivore and so, being inaccessible, remain outside a food chain from which size alone does not preclude them. During the time that the Megalopa Larvæ of Corystes were swarming in Plymouth waters, all the fishes which could catch them were feeding upon them to a greater or less extent. But *Callionymus lyra* was feeding on them not at all. There is no reason to suppose that this fish would not or could not eat the larvæ had they been available to it. The Megalopas, judging from the type and size of the other organisms which Callionymus will devour, are not too large or too small to suit it, nor is the fish too sluggish to catch them. But, so far as can be determined from observations on the habits of the fish, it never in ordinary circumstances leaves the bottom to feed. Therefore Megalopas swarming in the waters above it (**21**, p. 602) would not come within its range at all. Rays also are largely bottom feeders, but they will not infrequently rise off the ground in pursuit of food. Thus they,

the younger stages especially, made use of the Megalopas during the short time that they were abundant in the sea (Table II, p. 695).

Aquatic carnivores differ also from the majority of terrestrial forms in that they show a marked change of food (*prey*) with growth. This is due to at least two important factors. The first is that the larval fish must "fend for itself" from the time that the yolk-sac is absorbed, or even before, being entirely dependent upon its own efforts for the capture of its food. These little juvenile fishes must of necessity feed upon organisms proportionate to their size, which may be the young stages of the same food animals that support the adult fish or entirely different organisms. The food and feeding habits of the larval and post-larval stages of fishes have been very fully investigated by Lebour (*op. cit.*) and need not therefore be detailed here. Gradual change in the optimum size of food with growth continues until the adult size is reached. Todd (**29**) states that young Cod in the North Sea feed wholly on Crustacea, chiefly Ampelisca. With increase in size, their diet includes other groups, especially Pisces, Mollusca, and Polychæta. Young Plaice (<10 cm.) feed chiefly on Crustacea (Amphipoda, etc.) and Polychæta. With increase in size, Mollusca take first place. Such examples need not be multiplied. Among fishes captured on the "corner" grounds, change of food with growth was most obvious in two species of Ray—*Raia clavata* and *R. maculata*. The food of the young stages (20–40 cm.) consisted mainly of small Crustacea, chiefly Ampelisca.* Larger fish fed less upon Ampelisca and depended more upon other larger Crustacea. Eventually, in the largest fish, Amphipoda disappear entirely from their diet (Table II).

The prey of many terrestrial carnivores, on the other hand, changes but little or not at all during their growing period for the simple reason that they do not hunt. To begin with, the young of predatory mammals, for example, are fed upon maternal milk. Later on, the parents forage on their behalf, carrying home prey to the lair to feed them. Thus the growing animal does not have to hunt for itself until, from the point of view of foraging for food, it has become an adult and can catch the normal prey of the species. This applies also to birds. The nestlings are fed either upon semi-digested regurgitations from the stomach of the parent (e.g. Penguins) or are supplied liberally with food brought back by the old birds to the nest. In short, the higher terrestrial carnivores at least, do not have to depend upon their own efforts from the moment of their birth. This the little fish is obliged to do or die.

In the sea, another important factor bringing about change of food with growth is, in many cases, the change of level or environment frequented by the growing fish at different stages of its development. It

* During the time that Corystes Megalopas were abundant, young Rays (20–30 cm.) were feeding largely upon them (Table II).

Food of *Raia clavata* and *Raia maculata*.

Total number of Organisms in all Stomachs Examined.

	Season.	Length of Fish (in cm.).	Ampelisca.	Other Amphipoda.	Corystes Megalopas.	Schizopoda.	Isopoda.	Porcellana longicornis.	Annelida.	Hippolytidæ.	Portunus pusillus.	Crangonidæ.	Pandalidæ.	Galathea.	Upogebia.	Amphioxus.	Pisces.	Inachidæ.	Eupagurus.	Atelecyclus & Corystes.	Portumus depurator.	Total Number of Fishes Examined.
Raia clavata	Winter.	>10	**11**	–	–	**15**	–	–	2	3	–	1	5	–	1	–	1	–	–	–	1	8
		>20	**236**	3	–	1	–	6	–	1	–	1	1	1	1	–	1	–	–	–	1	11
		>30	**167**	–	–	–	–	–	1	2	2	7	**29**	–	**11**	–	12	–	–	–	12	19
		>40	2	–	–	–	–	–	–	1	8	1	**25**	–	4						7	8
		>50	1	–	–	–	–	–	–	–	1	1	9	6	**14**	–	2	–	**13**	3	**76**	25
		>60	–	–	–	–	–	–	–	–	–	–	–	–	2	–	4	–	5	1	**23**	9
	Summer.	>10	8	–	**78**	5	1	–	1	1	2	1	–	–	–			–		–	–	12
		>20	3	–	**89**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5
		>30	**69**	–	**477**	–	–	–	3	1	4	4	8	1	–						2	23
		>40	**11**	–	**183**	–	–	–	–	–	3	1	7	**13**	9	–	1		–	2	**11**	16
		>50	–	–	**29**	–	–	–	3	–	–	–	4	**19**	**14**	–	1	–	9	2	**49**	25
		>60	–	–	–	–	–	–	–	–	–	–	–	**11**	7		–	–	4	1	2	6
Raia maculata	Winter.	>20	**15**	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	2
		>30	**296**	–	–	–	**30**	–	–	2	2	1	1	2	4	–		–		–	–	13
		>40	3	–	–	–	–	–	–		–	–	1	–	1	–	3	–		–	8	5
		>50	1	–	–	–	–	–	–	–	–	–	3		2	–	**3**	–	–	1	4	5
		>60	–	–	–		–	–		–	–	–	–	1	–	–	–	–	1	2	8	3
	Summer.	>20	3	2	13	–	–	–	2	–	2	–	–	–		–	–	–	–	–	–	1
		>30	113	3	150	4	2	4	6	–	–	4		–	–	–	–	–	–	–	–	6
		>40	13	1	209	1	–	–	4		–	1	–	–	–	10	–	–	–	–	–	3
		>50	3	–	–	–	–	1	–	–	1		–	2	5	–	–	2	**14**	3	9	11
		>60	–	–	–	–	–	–	–	–	–	–	–	–	3	–	3	3	4	1	2	6

* This table shows :—

(a) Gradual change of food with growth.

(b) That Ampelisca was abundantly available to the Rays in the winter season when few were taken in the bottom sampler.

(c) That the younger stages preyed largely upon Corystes Megalopas when these larvæ were swarming in the area in summer.

will suffice to quote one example. Young Pleuronectidæ before metamorphosis are active members of the marine macro-plankton, feeding greedily upon other plankton organisms of suitable size. Later, when metamorphosis sets in, they descend to the sea bottom and there remain lying on one side for the rest of their lives. It is obvious, therefore, that apart altogether from any change imposed by increase in size, there must follow a complete change of food due to change of environment and therefore of available food organisms.

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APPENDIX.

Tables III, IV, and V.

Explanation of Tables.

Table III. Bottom Sampler Hauls.

In this table is recorded the number of individuals or homogeneous groups of animals brought up from 0·5 square metre of bottom in five hauls of the 0·1 square metre bottom sampler at all stations 1–15. (See Chart, p. 678.)

The type of soil* at each station is indicated. Seasonal observations are tabulated under the heading a, b, c, d for autumn 1928, and the following winter, spring and summer respectively.

Points of special interest in this table are :—

(a) The relatively large Polychæte fauna of the area (see p. 689).

(b) The almost complete absence of Ampelisca in the winter season in bottom sampler hauls (see p. 681).

(c) The more or less uniform distribution of Upogebia spp. over the whole area as recorded by the bottom sampler—probably only a small fraction of the whole population (see p. 682).

(d) Mollusca are poorly represented on this ground.

(e) *Portunus depurator* is not recorded at all by the bottom sampler.

(f) That there is little or no change in the infauna as a whole over the year.

In this and the following table, where for various reasons actual counts were impracticable or impossible, the following signs have been used.

+ =Fragments only of the animal were obtained.
⊕ =Present, but not counted.
‡‡ =Present.

Table IV. Trawl Samples.

This table records the number of individuals or homogeneous groups of the epifauna per ¼ acre of bottom as brought up by the "Agassiz" trawl. Four ¼-acre hauls are given for each of stations 3, 10, 12, and 14 towing north, south, east, and west (N.S.E.W.) in turn from each of these centres. Three seasons' observations are indicated, as explained for Table III, by the letters b, c, d at the heads of the columns.

Points of special interest brought out by this table are :—

(a) The relative abundance of *Pandalina brevirostris*, and the migratory movements thereof (see p. 680).

* Detailed analyses of the soils have not been made, but samples are preserved so that this can be done later if necessary.

(b) *Portunus depurator* is very common on the ground, although not one was captured by the bottom sampler.

(c) A sudden appearance of *Acanthodoris pilosa* around station 3 when the summer series of observations was taken; other Nudibranchs also more numerous.

(d) *Crangon vulgaris* is most numerous on the ground in winter, having left its summer haunts closer inshore. *Pontophilus spinosus* is also present in greatest numbers at this season.

(e) Scarcity of *Corystes cassivelaunus* and *Atelecyclus septemdentatus*. In this connection, cf. Table I, page 684.

Table V. Food of Fishes.

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Stat	12			13				14				15			
Type o				Mud, containing some very fine sand.											
	l.														
Seas	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
Asteroidea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Ophiuroidea	–	2	1	–	–	–	1	2	–	–	–	3	–	1	–
Echinoidea	1	1	–	–	–	–	–	1	–	–	–	3	–	–	–
Holothuroidea	–	1	–	4	+	1	2	–	1	–	1	2	1	–	3
Nemertinea	–	1	–	+	–	–	1	1	+	+	–	–	+	–	1
Polygordius	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aphrodite aculeata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Harmothoë lunulata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Scalisetosus assimilis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sthenelais boa	2	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Sthenelais limicola	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phyllodoce sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eulalia ornata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ophiodromus flexuosus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nephthys cæca	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–
Nephthys hombergii	3	2	5	3	3	–	1	4	3	4	3	8	3	9	4
Glycera convoluta	–	1	1	2	2	1	4	4	1	–	3	4	3	–	2
Goniada maculata	–	–	–	8	–	1	1	–	1	–	1	3	–	–	3
Nematonereis unicornis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hyalinœcia bilineata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lumbriconereis spp.	–	3	–	–	–	–	–	–	–	2	1	–	–	–	1
Aricia cuvieri	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Laonice cirrata	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Magelona papillicornis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phyllochætopterus anglica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Heterocirrus spp.	–	–	–	1	–	–	–	–	–	–	–	2	–	–	–
Scalibregma inflatum	–	–	–	3	–	1	–	1	–	–	–	–	–	–	–
Notomastus latericeus	+	3	3	1	3	3	11	5	–	1	5	2	2	–	9
Clymene sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Owenia fusiformis	3	6	–	3	–	1	5	5	1	6	1	5	2	3	6
Pectinaria auricoma	–	–	–	8	–	–	6	3	–	1	3	5	–	–	–
Amphicteis gunneri	–	1	–	4	–	1	–	–	–	1	–	–	–	–	–
Melinna palmata	–	5	–	6	–	1	5	4	–	–	–	–	1	4	3
Loimia medusa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lanice conchilegica	1	1	–	–	–	–	1	–	–	–	–	–	–	1	–
Thelepus cincinnatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Polycirrus caliendrum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Terebellides stroemi	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sabella pavonina	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–
Dasychone bombyx	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hydroides norvegica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pomatoceros triqueter	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gephyrea	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Scalpellum vulgare	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ampelisca spp.	2	9	25	30	–	30	20	53	–	79	21	49	–	8	30
Perioculodes longimanus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cheirocratus sundevalli	–	–	–	1	–	–	–	2	–	–	–	1	–	–	–
Maera othonis	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–
Gammarus sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Photis longicaudata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Erichthonius brasiliensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Conilera cylindracea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diastylis sp.	–	1	–	5	–	1	–	–	–	–	–	2	1	–	–
Squilla larva	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Alpheus ruber	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1
Processa canaliculata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Galathea nexa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Galathea intermedia	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Upogebia stellata	–	–	2	–	–	–	–	–	–	–	–	–	–	–	2
Upogebia deltaura	–	–	1	2	–	2	–	1	–	–	2	2	–	–	5
Callianassa subterranea	–	–	5	5	3	1	10	4	1	1	4	–	–	1	6
Paguridæ	–	–	–	–	–	–	–	2	–	–	–	–	–	–	1
Porcellana longicornis	–	–	–	–	–	–	1	–	–	1	–	1	–	–	–
Ebalia cranchii	–	–	–	1	–	–	1	–	–	1	1	3	1	–	1
Ebalia tuberosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Macropodia longirostris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Inachus dorsettensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Portunus pusillus	–	–	1	2	–	–	–	–	–	–	–	3	–	–	–
Atelecyclus septemdentatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gonoplax rhomboides	–	–	–	1	–	–	–	–	–	–	1	–	–	–	1
Craspedochilus onyx	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Turritella communis	1	–	–	3	2	–	4	–	–	2	–	3	4	1	3
Nucula nucleus	2	2	–	–	–	–	–	–	1	–	–	–	–	–	–
Nucula nitida	–	–	1	2	1	–	–	–	–	–	–	–	–	–	–
Nucula radiata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Glycymeris glycymeris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Æquipecten opercularis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Palliolum tigerinus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Astarte sulcata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lucina spinifera	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Lucina borealis	–	–	1	2	–	–	1	–	–	–	–	–	–	–	–
Syndosmya alba	–	1	–	11	1	–	–	5	–	–	1	3	1	–	–
Tellina crassa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Tellina donacina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lucinopsis undata	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Dosinia exoleta	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Clausinella fasciata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ventricola casina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Timoclea ovata	9	2	–	1	–	–	–	–	–	–	–	–	–	1	–
Chamelæa gallina	–	–	–	1	5	–	–	2	1	–	–	–	–	–	–
Cardium sp.	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Psammobia tellinella	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Corbula gibba	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–
Solecurtus antiquatus	–	–	–	–	1	–	1	–	–	–	–	1	–	–	–
Cultellus pellucidus	–	–	1	7	1	1	2	3	1	1	1	7	2	2	3
Natica alderi	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

(b) *Portunus depurator* is very common on the ground, although not one was captured by the bottom sampler.

(c) A sudden appearance of *Acanthodoris pilosa* around station 3 when the summer series of observations was taken; other Nudibranchs also more numerous.

(d) *Crangon vulgaris* is most numerous on the ground in winter, having left its summer haunts closer inshore. *Pontophilus spinosus* is also present in greatest numbers at this season.

(e) Scarcity of *Corystes cassivelaunus* and *Atelecyclus septemdentatus*. In this connection, cf. Table I, page 684.

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Station.	1				2				3				4				5				6				
Type of Soil.	Clean shelly gravel.				Medium shell gravel, mixed with mud and pebbles.				Rough shell gravel mixed with mud and pebbles.												Medium gravel mixed with mud. Some pebbles.				
Season.	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a
Asteroidea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ophiuroidea	–	–	1	–	–	–	2	1	–	–	–	3	–	–	–	–	–	–	–	1	–	–	1	1	1
Echinoidea	1	1	2	–	–	–	–	1	4	–	–	1	5	–	2	–	–	–	–	–	–	–	–	–	1
Holothuroidea	1	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	2	–	–	1	–	1	1	–	–
Nemertinea	1	–	1	–	1	–	–	–	2	1	–	+	1	1	–	–	1	+	+	+	–	+	–	–	1
Polygordius	1	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Aphrodite aculeata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Harmothoë lunulata	1	–	–	–	–	–	–	–	1	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–
Scalisetosus assimilis	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sthenelais boa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sthenelais limicola	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phyllodoce sp.	–	–	–	–	–	–	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	1
Eulalia ornata	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Ophiodromus flexuosus	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nephthys cæca	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nephthys hombergii	2	2	2	–	–	1	–	–	–	–	–	–	2	–	–	–	2	–	–	–	–	1	–	1	3
Glycera convoluta	4	3	–	1	1	2	1	1	2	4	2	1	1	2	–	–	1	1	–	–	4	1	2	–	2
Goniada maculata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–
Nematonereis unicornis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–
Hyalinœcia bilineata	–	1	–	1	3	–	–	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–
Lumbriconereis spp.	2	–	–	1	1	–	3	–	4	–	2	2	8	4	4	5	2	–	4	1	5	1	–	3	5
Aricia cuvieri	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Laonice cirrata	–	1	–	1	–	–	–	–	1	–	–	–	1	–	1	–	–	–	1	–	–	–	–	–	–
Magelona papillicornis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phyllochætopterus anglica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	3	–
Heterocirrus spp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
Scalibregma inflatum	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–
Notomastus latericeus	–	–	–	–	+	–	4	–	5	–	3	+	+	1	5	3	1	1	1	1	2	–	+	4	+
Clymene sp.	–	–	–	–	–	–	–	–	–	–	–	+	1	–	–	+	–	–	–	–	2	–	–	+	–
Owenia fusiformis	2	2	4	–	2	–	–	–	–	1	–	–	9	–	2	–	8	–	4	9	7	8	5	5	6
Pectinaria auricoma	–	1	–	–	–	–	–	–	–	–	1	–	1	–	–	–	2	1	2	–	1	–	–	–	1
Amphicteis gunneri	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	3	–	–	–	1	–	–	–	–
Melinna palmata	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	3	1	6	–	1	3	–
Loimia medusa	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	4	–	–	–	–
Lanice conchilegica	–	–	1	–	1	–	–	–	–	1	2	2	1	1	–	–	–	–	–	1	–	–	–	–	2
Thelepus cincinnatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Polycirrus caliendrum	1	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Terebellides stroemi	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Sabella pavonina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–
Dasychone bombyx	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hydroides norvegica	–	–	–	–	⊕	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pomatoceros triqueter	–	–	–	–	⊕	⊕	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gephyrea	–	–	–	–	1	1	–	–	2	–	–	1	–	–	–	1	1	–	–	–	2	–	1	–	1
Scalpellum vulgare	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	⊕	–	–	–	–	–
Ampelisca spp.	2	–	4	1	6	1	2	1	2	1	2	1	2	1	–	–	3	–	–	–	2	–	2	5	1
Perioculodes longimanus	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Cheirocratus sundevalli	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Maera othonis	1	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	2	1	–	1
Gammarus sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Photis longicaudata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	3	–
Erichthonius brasiliensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Conilera cylindracea	–	–	–	1	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diastylis sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Squilla larva	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Alpheus ruber	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Processa canaliculata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Galathea nexa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	1	1
Galathea intermedia	2	–	1	–	1	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	1	1
Upogebia stellata	1	–	2	–	1	1	1	2	–	1	–	2	–	–	3	2	1	1	1	–	1	1	2	–	–
Upogebia deltaura	–	–	1	–	–	–	–	–	1	1	3	–	–	1	–	2	1	1	1	3	1	2	4	1	–
Callianassa subterranea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Paguridæ	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Porcellana longicornis	–	–	–	–	–	1	–	–	–	3	–	–	–	–	–	1	–	–	–	–	–	–	–	3	–
Ebalia cranchii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	2	–	2	–	1	–	–
Ebalia tuberosa	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–
Macropodia longirostris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Inachus dorsettensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Portunus pusillus	1	–	–	–	2	1	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	1
Atelecyclus septemdentatus	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Gonoplax rhomboides	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Craspedochilus onyx	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	1
Turritella communis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	3
Nucula nucleus	1	3	–	–	3	–	2	2	1	4	5	–	1	–	1	–	–	–	1	1	9	–	1	1	4
Nucula nitida	–	–	1	–	1	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–
Nucula radiata	–	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Glycymeris glycymeris	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Æquipecten opercularis	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Palliolum tigerinus	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Astarte sulcata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Lucina spinifera	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lucina borealis	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Syndosmya alba	1	–	–	1	–	–	–	–	–	2	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–
Tellina crassa	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Tellina donacina	–	–	–	–	1	1	–	–	1	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Lucinopsis undata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dosinia exoleta	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Clausinella fasciata	2	1	1	–	–	1	1	1	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–
Ventricola casina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Timoclea ovata	–	–	–	–	1	–	11	2	–	2	1	–	5	–	2	–	–	–	–	–	3	–	–	–	1
Chamelæa gallina	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–
Cardium sp.	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Psammobia tellinella	1	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Corbula gibba	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Solecurtus antiquatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Cultellus pellucidus	–	–	3	–	–	–	–	–	–	–	–	–	1	–	3	–	–	–	–	–	–	1	–	–	–
Natica alderi	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–

7	8	9	10	11	12	13	14	15
Fine silty sand, with pebbles, shells, and shell fragments.			Very fine muddy sand.			Mud, containing some very fine sand.		

b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
1	1	1	–	–	1	1	–	–	4	–	2	–	–	2	1	–	3	–	–	–	2	1	–	–	–	1	2	–	–	–	3	–	1	–
1	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	–	–	–	–	–	1	–	–	–	3	–	–	–
–	1	1	–	–	–	1	–	–	1	3	–	1	1	1	–	–	1	1	3	–	1	–	4	+	1	2	–	1	–	1	2	1	–	3
–	–	+	–	–	3	–	–	1	–	1	–	–	1	1	–	1	+	2	–	–	1	–	+	–	–	1	1	+	+	–	–	+	–	1
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
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2	3	–	4	3	6	–	2	3	3	3	4	1	1	5	2	3	5	10	6	3	2	5	3	3	–	1	4	3	4	3	8	3	9	4
–	3	2	4	–	3	–	4	–	2	2	3	3	4	1	3	–	–	–	–	–	1	1	2	2	1	4	4	1	–	3	4	3	–	2
–	1	–	–	–	1	–	–	–	–	3	–	–	–	1	–	1	–	1	–	–	–	–	8	–	1	1	–	1	–	1	3	–	–	3
–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
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5	–	4	–	1	5	–	1	4	–	4	1	1	2	8	–	–	–	1	+	3	–	–	–	–	–	–	–	–	2	1	–	–	–	1
1	–	–	–	1	–	–	–	–	1	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
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+	2	2	–	2	6	+	3	3	4	+	+	4	2	1	–	2	–	1	+	3	3	1	3	3	11	5	–	1	5	2	2	–	9
–	+	–	–	–	–	+	–	–	–	+	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
3	14	5	5	7	5	3	2	8	–	12	2	5	–	11	4	3	3	6	3	6	–	3	–	1	5	5	1	6	1	5	2	3	6
–	–	–	–	3	–	–	–	1	–	2	–	1	1	–	–	1	1	–	–	1	–	4	–	1	–	–	–	1	–	–	–	–	–
–	1	–	1	–	–	–	15	10	5	2	4	3	3	–	3	4	1	–	5	–	6	–	1	5	4	–	–	–	–	1	4	3
–	–	1	–	–	–	1	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1	–	–	1	2	4	–	–	1	–	1	–	–	–	3	1	–	3	2	1	1	–	–	–	–	1	–	–	–	–	–	–	1	–
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1	2	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
–	⊕	–	–	–	–	–	–	–	–	–	–	–	⊕	⊕	–	–	⊕	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1	13	4	7	7	5	9	–	42	2	7	–	109	30	5	2	35	–	2	2	9	25	30	–	30	20	53	–	79	21	49	–	8	30
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3	–	–	–	–	–	–	–	–	–	–	–	6	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
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–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
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1	–	–	–	–	1	3	–	–	1	–	–	1	–	–	–	1	2	–	–	–	1	2	–	2	–	1	–	–	2	2	–	–	2	5
–	–	–	1	–	1	2	1	9	9	–	–	7	1	–	–	3	3	–	–	–	5	5	3	1	10	4	1	1	4	–	–	1	6
–	1	4	–	1	–	–	–	1	–	–	–	–	–	1	–	2	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	1
–	–	–	–	–	2	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	1	–	–	–	–
–	1	1	–	–	–	–	2	1	–	–	–	–	–	–	1	1	–	–	–	–	–	1	–	–	1	–	–	1	1	3	1	–	1	–
–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
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–	2	–	–	–	–	–	–	1	–	1	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	1	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4	–	–	2	–	5	3	6	8	1	–	1	–	–	–	–	–	–	–	–	1	–	3	2	–	4	–	–	2	–	3	4	1	3
–	1	7	1	–	–	–	–	–	–	–	–	–	–	3	1	–	–	–	–	2	2	–	–	–	–	–	1	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	2	1	–	–	–	–	–	–	–	–	–	–	–
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2	–	4	–	1	–	–	–	–	1	–	–	–	2	1	–	1	–	–	–	–	1	2	–	–	1	–	–	–	–	1	–	–	–	–
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–	3	1	1	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	1	9	2	–	1	–	–	–	–	–	–	–	–	1	–	–	–
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1	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–
1	–	3	–	5	–	1	3	3	–	–	1	–	–	1	1	4	–	2	–	–	1	7	1	1	2	3	1	1	1	7	2	2	3
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Station.	3												10								
Direction Towed.	N.			E.			S.			W.			N.			E.			S.		
Season.	b	c	d	b	c	d	b	c	d	b	c	d	b	c	d	b	c	d	b	c	d
Hydractinia echinata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sertularella gayi	–	–	–	–	–	–	–	–	–	–	–	‡‡	–	–	–	–	–	–	–	–	–
Hydrallmania falcata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Antennularia antennina	–	–	–	–	–	–	–	–	‡‡	–	–	‡‡	–	–	–	–	–	–	–	–	–
Plumularia catharina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Alcyonium digitatum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Metridium senilis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Astropecten irregularis	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Palmipes membranaceus	–	–	2	1	–	–	–	–	2	1	–	1	–	–	–	–	–	–	–	–	–
Solaster papposus	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Henricia sanguinolenta	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Stichastrella rosea	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Asterias rubens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Marthasterias glacialis	3	2	3	2	2	–	1	–	2	–	4	1	7	1	5	14	3	5	8	1	4
Ophiothrix fragilis	3	–	1	2	2	3	4	–	7	1	5	6	2	2	4	–	–	17	1	–	1
Amphiura filiformis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ophiura texturata	8	–	10	6	–	–	3	–	1	1	–	–	–	–	1	2	1	1	2	–	1
Echinus esculentus	1	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Spatangus purpureus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Echinocardium cordatum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phascolion strombi	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Balanus sp.	⊕	⊕	⊕	–	⊕	⊕	–	⊕	⊕	–	⊕	–	⊕	–	⊕	–	⊕	⊕	⊕	–	–
Scalpellum vulgare	⊕	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Conilera cylindracea	6	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Schizopoda	–	–	–	–	3	–	–	6	–	–	7	–	–	–	–	–	–	–	–	–	–
Pandalus montagui	11	–	3	2	2	29	3	3	–	–	–	6	–	2	–	–	4	–	–	1	–
Pandalina brevirostris	21	121	50	24	116	421	–	429	6	18	377	173	16	1	7	19	18	4	62	1	–
Hippolyte varians	–	1	–	–	1	14	–	2	–	1	–	–	–	–	–	–	–	–	1	–	1
Spirontocaris cranchi	–	–	1	–	–	–	–	3	–	–	1	–	–	–	–	–	–	–	–	–	–
Leander serratus	–	–	–	–	–	–	–	4	–	–	–	–	–	2	–	–	2	–	–	1	–
Crangon vulgaris	8	–	–	–	1	–	2	–	–	5	–	–	28	–	–	36	–	1	23	–	–
Philocheras sculptus	1	2	–	–	2	4	–	8	2	1	–	2	–	–	–	–	–	–	–	–	–
Philocheras bispinosus	–	1	–	–	2	4	–	2	–	1	2	2	–	–	–	–	–	–	–	–	–
Pontophilus spinosus	–	2	2	–	1	1	–	2	–	6	1	–	20	–	4	45	2	2	20	–	1
Galathea nexa	9	–	4	1	2	11	6	8	15	4	13	9	9	6	9	7	8	12	21	4	15
Galathea intermedia	3	–	–	2	–	2	3	–	10	1	–	–	4	–	2	–	–	3	6	–	1
Munida bamffica	–	–	–	–	–	–	–	1	–	–	2	–	–	–	1	–	–	–	–	–	–
Porcellana longicornis	1	3	10	4	3	7	16	10	20	4	14	1	12	8	7	4	12	23	14	2	–
Eupagurus bernhardus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	2	–	1	–
Eupagurus prideauxi	24	2	4	7	5	16	10	21	53	14	12	–	12	2	–	68	2	–	75	1	–
Anapagurus lævis	12	–	–	3	–	–	–	–	–	–	–	5	–	–	–	–	–	8	–	–	–
Portunus puber	–	–	–	–	–	–	–	–	–	–	–	1	1	1	1	–	–	–	–	2	–
Portunus pusillus	6	–	2	–	–	–	2	–	5	–	–	2	–	–	–	1	–	–	1	–	–
Portunus holsatus	1	2	3	2	2	4	1	3	6	–	2	–	–	–	–	–	2	1	–	1	1
Portunus depurator	21	26	30	4	10	23	6	11	22	8	15	35	41	14	15	56	29	35	80	51	42
Cancer pagurus	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–
Atelecyclus septemdentatus	–	1	1	–	–	–	1	–	1	–	–	1	–	1	–	–	–	–	1	–	1
Corystes cassivelaunus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gonoplax rhomboides	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	1	–	–	–	1
Ebalia tuberosa	3	1	1	–	–	1	2	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Ebalia cranchii	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	2	–	–	–	–
Maia squinado	–	–	–	–	–	–	–	–	–	–	2	–	1	–	–	–	–	–	–	–	–
Eurynome aspera	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hyas araneus	–	–	–	–	–	2	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Inachus dorsettensis	13	6	10	4	2	11	4	2	8	–	–	15	11	2	2	27	2	5	8	3	6
Macropodia longirostris	25	10	31	24	8	107	1	16	16	13	12	64	21	4	11	61	6	16	40	4	15
Macropodia rostratus	3	1	5	4	2	9	–	3	1	–	2	–	3	1	1	2	1	3	3	2	1
Phoxichilus spinosus	–	2	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	1
Ovula patula (on Alcyonium)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Natica alderi	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Turritella communis	–	–	–	–	–	–	–	–	–	–	–	–	3	1	7	5	6	2	2	4	1
Oscanius membranaceus	–	–	–	–	–	4	–	1	2	–	2	4	2	–	–	–	–	–	–	–	1
Amphorina cærulea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–
Galvina tricolor	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Antiopella hyalina	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Lomanotus sp.	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Dendronotus frondosus	–	1	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–
Pleurophyllidia loveni	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Archidoris tuberculata	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–
Jorunna johnstoni	–	–	–	–	–	1	–	–	1	–	–	2	–	–	1	–	–	–	–	–	–
Platydoris testudinaria	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Polycera quadrilineata	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–
Acanthodoris pilosa	–	–	1	–	–	14	–	–	2	–	–	21	–	–	–	–	–	–	–	–	–
Lamellidoris oblonga	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ancula cristata	–	–	–	–	–	5	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–
Lamellibranchs	16	–	17	2	2	13	10	–	22	3	4	6	–	–	2	2	–	2	1	1	1
Sepia officinalis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Sepiola atlantica	1	1	2	–	–	–	–	1	2	–	–	–	–	–	–	–	–	–	2	–	–
Eugyra arenosa	–	–	4	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ascidiella scabra	1	–	–	–	–	1	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–
Polyzoa	–	–	–	–	–	‡‡	–	–	–	–	–	‡‡	–	–	‡‡	–	–	–	–	–	–
Amphioxus lanceolatus	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

IV.

	12															14														
W.				N.			E.			S.			W.			N.			E.			S.			W.						
b	c	d	b	c	d	b	c	d	b	c	d	b	c	d		b	c	d	b	c	d	b	c	d	b	c	d			
–	–	–	–	–	–	–	–	–	–	–	–	‡‡	–	–		–	–	–	–	–	–	–	–	–	–	–	–			
–	–	–	‡‡	–	–	–	–	–	‡‡	–	–	–	–	–		–	–	–	–	–	–	–	–	‡‡	‡‡	–	–			
–	–	–	–	–	–	–	–	–	‡‡	–	‡‡	–	–	–		–	–	–	–	–	–	–	–	–	‡‡	–	‡‡			
–	–	–	‡‡	–	–	–	–	–	‡‡	–	‡‡	–	–	–		–	–	–	‡‡	–	–	‡‡	–	–	‡‡	–	–			
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–	‡‡			
–	–	–	–	–	–	–	–	–	–	–	‡‡	–	–	–		–	–	–	–	–	–	–	–	–	–	–	–			
–	–	–	–	1	–	–	–	–	–	–	1	–	2	–		2	–	–	–	–	–	–	–	1	1	–	2			
–	1	–	1	–	–	–	–	2	–	–	–	–	1	–		–	–	–	–	–	–	–	–	–	–	–	–			
–	–	–	–	–	–	–	–	–	–	–	–	–	–

TABLE V.

Name of Fish.	Length (in cm.).	Ophiuroidea.	Echinoidea.	Holothuroidea.	Polychæta.	Cumacea.	Amphipoda.	Isopoda.	Schizopoda.	Palæmonidæ.	Pandalidæ.	Hippolytidæ.	Alpheidæ.	Crangonidæ.	Processa.	Calathea.	Typhlogebia.	Paguridæ.	Porcellana.	Ebalia.	Inachidæ.	Portunus.	Ateleocyclus.	Gonoplax.	Corystes.	Corystes Megalopas.	Mollusca.	Polyzoa.	Pisces.	Stomach Empty.	Total number of Fishes examined.
Trigla lineata	>5	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	2	–	–	–	–	–	–	–	–	–	–	2	
		–	–	–	–	–	*2*	–	–	–	–	–	–	–	–	*1*	–	–	*1*	–	–	–	–	–	–	–	–	–	–	*1*	*3*
	>10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1
		–	–	–	–	–	*1*	–	–	–	–	–	–	–	–	–	–	–	*2*	–	–	–	–	–	–	–	–	–	–	–	*2*
	>15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	2	–	–	1	–	–	–	–	–	–	–	–	2
		–	–	–	–	–	*1*	–	*1*	–	–	–	–	*1*	–	*2*	–	–	*1*	–	–	*1*	–	–	*1*	*1*		–	–	–	*2*
Trigla cuculus	>5	–	–	–	–	–	4	–	3	–	5	2	–	–	–	6	–	–	7	–	–	–	–	–	–	–	–	–	–	3	21
		–	–	–	–	–	*3*	–	*1*	–	*4*	–	–	–	–	*5*	–	–	*9*	*1*	–	*1*	–	–	–	–	–	–	–	–	*17*
	>10	–	–	–	–	–	7	–	–	–	12	1	–	11	–	6	1	–	–	–	–	8	2	–	–	–	–	–	2	5	28
		–	–	–	–	*5*	*15*	–	–	–	–	–	–	*5*	–	*4*	–	*1*	*16*	*1*	–	–	–	–	–	–	*1*	–	*1*	–	*24*
	>15	–	–	–	–	–	7	–	–	–	4	–	–	1	–	3	–	–	8	–	–	2	–	–	–	–	–	–	–	–	12
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	*4*	–	–	*1*	*2*	–	–	–	–	–	–	–	–	*1*	*1*	*6*
	>20	–	–	–	–	–	5	–	–	–	10	–	–	12	1	3	–	–	1	–	–	7	–	1	–	–	–	–	3	2	17
		–	–	–	–		*1*	–	*1*	–	*2*	–	–	*3*	–	*8*	*1*	*1*	*3*	–	–	*1*	–	–	–	–	*1*	–	*2*	–	*10*
Trigla hirundo	>15	–	–	–	–	–	1	–	–	–	1	1	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		3
		–	–	–	–	–	*1*	–	–	–	*1*	–	–	*2*	–	*2*	–	–	*1*	–	–	–	–	–	–	–	–	–	–	*1*	*3*
	>20	–	–	–	–	–	1	–	–	–	2	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	4
		–	–	–	–	–	–	–	–	–	*1*	–	–	*2*	–	*3*	–	–	*3*	*2*	–	*2*	–	–	–	–	–	–	–	–	*5*
Trigla gurnardus	>5	–	–	–	–	1	7	–	–	9	6	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13
		–	–	–	–	–	*9*	*1*	–	*7*	*3*	–	–	*1*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*10*
	>10	–	–	–	–	–	1	1	1	–	8	2	–	17	–	9	–	–	–	–	–	–	–	–	–	–	–	–	1	1	21
		–	–	–	–	–	*4*	*1*	–	–	*6*	*1*	–	*11*	–	*5*	–	*1*	*1*	–	–	–	–	–	–	*1*	–	–	–	*3*	*13*
	>15	–	–	–	–	–	3	–	–	–	5	–	–	11	–	4	–	–	–	2	–	–	–	–	–	–	–	–	–		12
		–	–	–	–	–	*2*	–	–	–	*9*	–	–	*8*	*1*	*6*	–	–	–	–	–	*1*	–	–	–	–	–	–	–	*1*	*10*
	>20	–	–	–	–	–	–	–	–	–	5	–	–	2	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	1	7
		–	–	–	–	–	–	–	–	–	*1*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*1*	–	–	*2*	*1*	*3*
Lophius piscatorius	>20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	3
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*1*	–	*1*
	>30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*1*	-	*1*
	>40	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	6
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*9*	-	*9*
	>50	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	-	2
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*6*	*1*	*7*
	>60	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11	6	17
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*9*	*1*	*10*

Name of Fish.	Length (in cm.).	Ophiuroidea.	Echinoidea.	Holothuroidea.	Polychæta.	Cumacea.	Amphipoda.	Isopoda.	Schizopoda.	Palæmonidæ.	Pandalidæ.	Hippolytidæ.	Alpheidæ.	Crangonidæ.	Processa.	Galathea.	Upogebia.	Paguridæ.	Porcellana.	Ebalia.	Inachidæ.	Portunus.	Atelecyclus.	Gonoplax.	Corystes.	Corystes Megalopas.	Mollusca.	Polyzoa.	Pisces.	Stomach Empty.	Total number of Fishes examined.
Zeus faber	>5	–	–	–	–	–	–	–	1	–	3	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	6
		–	–	–	–	–	–	–	–	–	*1*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*5*	–	*5*
	>10	–	–	–	–	–	–	–	–	1	–	–	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	3	17
		–	–	–	–	–	–	–	–	–	–	–	*1*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*9*	*1*	*10*
	>15	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	1	7
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*5*	–	*5*
	>20	–	–	–	–	–	–	–	–	–	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	10	6	18
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*1*	–	*1*
Callionymus lyra	>5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
	>10	1	–	–	3	–	2	–	–	–	–	–	–	–	–	3	3	–	4	–	–	1	–	–	–	–	3	–	–	2	15
		3	–	–	*1*	–	*4*	–	–	–	–	–	–	–	–	*1*	*2*	*1*	*1*	*1*	–	–	–	–	–	–	*5*	–	–	*1*	*11*
	>15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	4	–	–	1	3	–	–	–	–	10	–	–	5	25
		1	–		–	–	*1*	–	–	–	–	–	–	–	–	–	*3*	*2*	*4*	–	*1*	*6*	–	–	–	–	*13*	–	–	*2*	*25*
	>20	4	–	–	1	–	–	–	–	–	–	–	–	–	–	–	5	3	6	–	–	5	–	–	–	–	9	–	–	–	15
		–	–	–	*3*	–	–	–	–	–	–	–	–	–	–	–	*1*	*5*	–	–	–	*3*	–	–	–	*1*	*10*	–	–	*1*	*18*
Cepola rubescens	>30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	3	
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*2*	*2*	
	>40	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	5	
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*4*	*4*	
	>50	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*7*	*7*	
Gadus luscus	>10	–	–	–	2	–	–	–	–	–	3	1	–	1	–	8	9	4	3	–	1	7	1	–	–	–	–	4	–	25	
		–	–	–	*1*	–	–	–	–	–	*4*	–	–	–	–	*7*	*6*	*5*	*4*	*1*	–	*9*	–	–	–	–	–	1	*5*	*1*	*25*
	>15	–	–	–	1	–	–	–	–	–	–	–	–	–	–	5	7	1	8	–	1	12	–	–	–	–	–	–	–	–	25
		–	–	–	*2*	–	–	*1*	–	–	–	–	–	–	–	*8*	*3*	*3*	*6*	*1*	*1*	*11*	–	–	–	*7*	–	–	*1*	–	*25*
	>20	–	–	–	–	–	–	–	–	–	5	–	–	–	–	12	1	1	2	5	–	9	–	–	–	–	–	–	9	4	25
		–	–	–	*3*	–	–	*1*	–	–	*1*	*1*	–	–	–	*13*	*14*	*4*	*4*	*1*	*2*	*5*	*2*	–	–	*3*	*1*	*1*	*1*	–	*25*
	>30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	2	3	–	–	3	1	–	–	–	–	–	3	–	5
		–	–	–	*1*	–	–	–	–	–	*1*	–	–	–	–	–	*3*	*1*	*1*	*1*	*1*	*4*	–	–	–	–	–	–	*1*	–	*8*
Gadus minutus	>5	–	–	–	–	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	>10	–	–	–	5	–	2	–	–	–	2	–	–	–	–	5	4	1	–	–	–	1	–	–	–	–	–	–	11	25	
		–	–	–	*3*	–	*1*	–	–	–	–	–	–	–	–	*3*	*2*	*4*	*1*	–	–	–	–	–	–	*21*	–	–	*2*	*2*	*25*
	>15	–	–	–	–	3	–	–	–	–	4	–	–	–	–	2	1	1	–	–	–	–	–	–	–	–	–	–	3	5	9
		–	–	–	*4*	–	*1*	–	–	–	*1*	–	–	*2*	–	–	*4*	–	–	–	–	–	–	–	–	*20*	–	–	*3*	*2*	*25*

Gadus merlangus	>5	–	–	–	–	–	–	–		–	–	–		–	–	–	–	–	–	–	–	·	–	–	–	2	–	–	17	1	19
	>10	·	–	–	1	–	–	·		–	–	–		4	–	–	1	·	·	–	–	2	·	–	–	–	–	–	14	–	17
	>15	–	–	–	–	–	–	–		–	–	–		–	–					–	–	–	–	–	–	23	·	–	–	2	25
	>20	–	–	–	·	–	–	–		–	–	–		–	–	–	–	–	–	–	–	·	–	–	–	–	–	–	–	–	–
		–	–	–	–	–	–	–	2	–	–	–		–	–	·		3	1	·					–	25	–	–	3	–	25
		–		·	1	–	2	–	·	–	–	–		–	–	·	10			–	–	–	–	–	–	–	–	–	14	10	25
		–	–	–	–	–	–	–		–	–	–		–	–	–	–	–	–	–					·	22	–	–	7	1	25
Merluccius vulgaris	>15	–	–	–	–	–	–		·	–		–			–	–	–	–	·					·		·		·	2	3	5
			–	–	–	–	–	–	–	–	–		–	–	·					–	–	·			–	–	–	–	–	–	–
	>20	–	–	–	–	–	–	–	–	–	–	–			–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	1	9
		–	–	–	–	–	·	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		·		–	6	1	7
	>30		–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–			·	·	–	9	3	12
		–	–		–			–	–	–		–	–	·	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	4
Rhombus lævis	>50	–	–	–	–	–	–	–	–		–				–	–	–		–	–	–	–	–	·	–	–	–	–	1	1	2
			–	–	–	–	–					–			–	–	–	–	·	–	–	–		·		–	–		1	–	1
Scophthalmus norvegicus	>5	–	–	–	1	1	2	–	3	–	3	2		6	1	2	–	–	–			–		–	–	–	–	–	–	7	25
		–	–		–	1	3	2	8		1		–	9	3	4	1	1	–	–	1	–	–	–	–	–	–	–	–	3	25
Arnoglossus laterna	>5	–	–	·	–	–	7		1	–	6	–		5	·	–				–	–	·			·		–	–	–	–	7
				–			4	1	1		5	–	–	7		·	–			–	–	–	–	·	·	–	–	·	–	–	9
	>10					2	42		6		–			35		–	–		–	–	6	–	–	–	–	2	4	1	50	
			–			1	1		3		1	·		1	–	1	–	–	4	–	–	2	–	–	–	4	–	–	13	1	25
	>15	–	–		·	–	4		1			–		8	·	·	·	–	2	–	–	1	–	–	–	–		–	1	–	8
		·	–		–	–	8			–		–		16		–	–	–	1		–	1	–		–	–	·	1	1	–	11
Lepidorhombus megastoma	>10						·	–	–		–	–		·		·	–		–	–	–	–	–	–	–	–	–	–	–	–	–
		–	–	–	–		–	–			–	–		–	–	·	–		–	–	–	·	–	–	–	–	–	–	1	–	1
	>15	·	·				–	–		–	–	·	–		–		–	·	–	–	–	·	·	–	–	–	–	–	–	–	–
			·	–	–		–	–	–	–	1		–	–	·	–			–	–	–	–	–	–	–	–	–	2	1	3
	>20		–		–	–		–		–	–	–	–	–					·	–	–	–	–	–	–	–	–	–	–	–	·
		·			·	·	–	·	–	–	–	–	–	–	·	·	–		–	–	–	–	–	–	–	–	–	1	1	2
Pleuronectes platessa	>20	–	–	–	2	–	–			·	·	–		·	–	1	5	·	–	–	–	–	–	–	–	1	–	–	3	10	
			–	–	1	–	1		·	–	·	–	–	·	–	–	3	–	–	–	–			·	2	4	–	–	2	7	
	>30	·	–	–	3	–	–	·	–	–		–	·	·	1	–	4	–	–	–	–	–		1	·	–	–	–	5	9	
		–	–		3	1	1	·	–	–		–		–	–	–	2	–	–	–	–				–	4	4	–	–	1	6	
	>40		·		–		–		–	–		–	–	–	–	–	–	–	–	–	–	·			·	–		–	–	1	1	
		–	·	–	3	–	–	–	·	–		–	·	–	–	–	–	–	–	–	·				–	–	5		–	1	6	
	>50			–	1		·	·	·	–		–		–	–	–	4	–	–	–	–	–	·			–	–	1	–	1	5	
		–	–		2		–		–	–	–	–	·	–	–	–	3	–	·	–		–	–	–	–	–	2	–	–	1	3	
Pleuronectes microcephalus	>20			–	23	–		–	–	–	–	–	·	·				–	–	–	–	–	–	–	–	–	–	–	–	2	25	
		–	–	–	24	–					–							–	–	–	–	–	–	–	–	–	–	–	–	1	25	
	>30	–	–	–	19			–			–			·	–	–	–	–	·	–	–	–	–	–	–	·	·	·	·	6	25	
		–	–	–	25													–		–	–	–	–	–	–	·	·	·	–	–	25	

Name of Fish.	Length (in cm.).	Ophiuroidea.	Echinoidea.	Holothuroidea.	Polychæta.	Cumacea.	Amphipoda.	Isopoda.	Schizopoda.	Palæmonidæ.	Pandalidæ.	Hippolytidæ	Alpheidæ.	Crangonidæ.	Processa.	Galathea.	Upogebia.	Paguridæ.	Porcellana.	Ebalia.	Inachidæ.	Portunus.	Ateleocyclus.	Gonoplax.	Corystes.	Corystes Megalopas.	Mollusca.	Polyzoa.	Pisces.	Stomach Empty.	Total number of Fishes examined.
Pleuronectes limanda	>10	3	–	–	6	–	–	–	–	–	–	–	–	–	–	4	4	1	1	–	–	6	–	–	–	3	1	–	4	16	31
		–	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11	25
	>15	3	–	–	1	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	1	–	–	–	–	2	–	2	2	8
		–	–	–	12	–	3	–	–	–	1	–	–	1	–	1	1	–	–	–	1	1	–	–	–	2	1	–	–	3	25
	>20	–	–	–	1	–	–	1	–	–	–	–	–	–	–	3	1	–	–	–	–	–	–	–	–	–	3	–	–	1	5
		–	–	–	9	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	3	–	–	–	–	–	–	–	2	11
Pleuronectes flesus	>20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	1
		–	–	–	2	–	–	–	–	–	–	–	–	–	–	1	1	–	1	–	–	–	–	–	–	–	2	–	–	1	3
Solea vulgaris	>20	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	2
		–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1
	>30	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	2	3
		–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2
	>40	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	1	–	–	1	3
		–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	1	–	–	1	4
Solea lutea	>5	–	–	–	–	–	3	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
		–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	–	–	1	5
Solea variegata	>5	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	8	11
		–	–	–	–	–	2	–	–	–	–	1	–	–	–	–	–	–	3	–	–	1	–	–	–	–	–	–	–	5	11
	>10	–	–	–	–	–	11	–	–	–	3	–	–	–	–	–	–	–	9	1	–	–	–	–	–	–	1	–	–	5	16
		–	–	–	10	–	4	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	5	15
	>15	–	–	–	2	–	4	–	–	–	1	–	–	–	–	–	–	–	2	–	–	1	–	–	–	–	1	–	–	3	7
		–	–	–	4	–	–	–	1	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	6
Conger conger	>60	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	2
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	3
Scyliorhinus canicula	>30	–	–	–	4	–	2	–	–	–	–	–	–	–	1	–	3	–	6	–	–	–	–	–	–	–	–	–	4	3	12
		–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	3	–	–	2	–	–	–	–	–	–	4	2	10
	>40	–	–	4	2	–	–	–	–	–	–	–	–	–	–	–	1	4	–	–	–	1	–	1	–	–	1	–	12	–	20
		–	–	–	5	–	–	–	–	–	–	–	–	–	–	–	2	5	1	–	1	3	–	1	1	–	1	–	11	1	25
	>50	–	–	–	10	–	–	–	–	1	–	–	–	–	–	–	8	7	–	–	2	1	–	–	–	–	4	–	14	–	28
		–	–	–	7	–	–	–	–	–	–	–	–	–	–	–	4	6	–	–	1	2	–	–	–	–	–	–	9	3	25
	>60	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9	–	–	3	4	–	–	–	–	1	–	10	–	11
		–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	11	–	–	6	5	–	–	–	–	–	–	15	1	21

	>10	–	–		1	–	2	–	–	–	2	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	3
		–	–	–	*1*	–	*3*	–	–	–	–	–	–	–	–	–	–	–	–	–			–	–	–	*3*	–	–	–	*2*	*5*
	>15	–			1	–	5	–	–	–	3	–	–	–	–	–	2	–	–	–	–	1		–	–	–	–	–	–	–	–	5
		–	–		–	–	*4*	*1*	*3*	–	–	–	–	*1*	–	–	–	–	–	–	*1*	–	–	–	*4*	–	–	–	–	–	7
	>20	–	–	–	1	–	7	–	1	–	1	–	–	1	–	1	–		2	–		–	–	–	–	–	–	–	–	–	–	11
				–	–	·	*2*	–	–	–	–	–	–	–	–	–	*2*	·	–	–	·	–	–	–	*1*	*2*	–	–	–	–	*5*
Raia clavata	>30	–			1	·	14	–	–	–	10	2	–	7	–	1	10	–	–	–	–	4	–	–		–	–	–	1	–	19
		–	–		*3*	–	*12*	–	–	–	*8*	*1*	–	*4*	–	*1*	–	–	–	–	–	*6*	–	–	–	*19*	–	–	*1*	–	*23*
	>40		–	–	–	–	2	–	–	–	4	1	–	1	–	–	4	–	–	–	–	7	–	–	·	–	–	–	–	–	8
		–	–	–	–	–	*4*	–	–	–	*3*	–	–	*1*	–	*7*	*8*		–	–	–	*11*	*2*	–	–	*12*	–	–	–	–	*16*
	>50	–	–	–	–	–	1	–	–	–	6	–	–	1	–	6	9	9	–	–	–	18	2	–	1	–	–	–	–	7	25
			–	·	*1*	–	–	–	–	–	*3*	–	–	–	–	*8*	*10*	*7*	–	–	–	*11*	*1*	–	·	*3*	–	–	*1*	–	*25*
	>60		–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	–	–	–	7	1	–	–	–	–	–	4	–	9
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	*3*	*6*	*4*	–	–	–	*1*	*1*	–	–	–	–	–	–	–	*6*
	>20	–		–	1	–	2	–	–	–	–	·	–	–	–	–	·	–	–	–	–	1	–	–	–	–	–	–	–	–	2
		–	–		*1*	*1*	*1*	–	–	–		–	–	–	–	–	–		–	·	–	*1*	–	–	–	*1*	–	–	–	–	*1*
	>30	–	–	–	1	–	12	1	–	–	1	1	–	1	–	2	4	–	–	–	–	2	–	–	–	–	–	–	–	1	13
		·	–	–	*4*	*1*	*6*	*2*	*2*	–	–	–	–	*4*	–	–	–	–	*2*	–	–	–	–	–	–	*6*	–	–	–	–	*6*
Raia maculata	>40	–		–	–	·	1	–	–	–	1	–	–	–	–	–	1	–	–	–	–	3	–	–	·	–	–	–	3	–	5
		–			*2*	·	*3*	–	*1*	–	–	–	–	*1*	–	–	–	–	–	–	–	–	–	–	·	*2*	–	–	–	–	*3*
	>50	–			·	–	1	–	–	–	–	–	–	–	–	1	–	1	–	–	5	2	–	·	–	–	–	–	–	–	5
		–	·		–	·	*1*	–	–	–	–	–	–	–	–	*1*	*3*	*9*	*1*	–	*1*	*7*	*2*	–	*1*	–	–	–	–	–	*11*
	>60	–	–		–	·	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	3	1	–	1	–	·	–	–	–	3
		–	–	·	–	·	–	–	–	–	–	–	–	–	–	·	–	*4*	–	–	*3*	*2*	*1*	–	–	–	–	–	*3*	–	*6*
	>20	–	–	–	*4*	–	–	–	–	–	1	–	–	4	–	–	–	–	1		–	3	–		–	–	–	–	4	–	7
		·	–	–	*3*	*1*	*3*	*1*	–	*1*	–	–	–	*1*	–	2	–	–	*1*	·	–	*1*	–	–	–	*3*	–		*1*	–	*4*
Raia nævus	>30	–	–		1	–	–	2	–	–	–	–	·	3	–	3	1	2	–	–	–	1	–	1	–	–	–	–	2	–	6
		–	–		*2*	–	*1*	–	–	–	–	*1*	–	*1*	–	*4*	*1*	–	–	*1*	·	–	–	·	*1*	*4*	–	–	–	–	*5*
	>40	·			1	–	–	–	–	1	–	–	–	1	–	2	2	4	–	1	–	4	–		–	–	–	–	–	–	5
		–			–	–	–	*3*	–	*1*	–	–	–	–	·	*3*	–	*5*	*1*	–	–	*1*	–	–	–	*2*	–	–	*1*	–	*6*
	>20	–		–		–	3		–	–	–	–	–	–	–	1	–	–	1	–	·	–	–	–	–	–	–	–	–	1	4
		·	–	–		–	*2*		–	–	–	–	–	–	–		*1*	–	*1*	–	–	–	–	–	–	–	–	–	–	*2*	*4*
	>30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Raia brachyura	>40	–	–	–	–	–	1	–	–	–	–	–	–	–	–	2	–	1	–	–	1	4	–	–	–	–	–	–	–	–	5
		–	–	–	–	–	*1*	–	–	–	–	–	–	*1*	–	*3*	–	*1*	–	–	–	*2*	–	–	–	*1*	–	–	–	*1*	*6*
	>50	–	–	–	–	–	2	–	–	–	–	–	–	–	–	1	1	–	–	–	–	1	–	–	–	–	–	–	–	–	3
		–	–	–	–	–	–	–	*1*	–	–		–	–	–	–	–	–	–	–	–	·	–	–	–	–	–	–	–	–	*1*

The Seasonal Abundance and Distribution of the Pelagic Young of Teleostean Fishes Caught in the Ring-Trawl in Offshore Waters in the Plymouth Area.

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With 2 Figures in the Text.

A LARGE number of collections were made with the 2-metre stramin ring-trawl in the years 1924, 1925 and 1926, to study the vertical distribution of young fish. Seeing that all these collections were made in exactly the same way, it was considered that they would form a good basis for a study of the quantitative differences in abundance of the different species at various times of the year. Accordingly, after 1926 the collections were supplemented in 1927, 1928 and 1929 by oblique hauls with the ring-trawl fishing at the same depths as those fished in the serial hauls in the study of the vertical distribution, that is the net was fished successively at the six different depths during half-an-hour's haul for 5 minutes at each depth. The results given in this report are all based on daylight catches.

In Table 3 are brought together the average monthly catches per half-hour's haul for each year for the post-larvæ of the various species. In the case of the 1924, 1925 and 1926 observations, which were based usually on six hauls each of ten-minutes' duration at six different depths, the total number of each species caught at all depths together at any one station is taken and from it the number caught per half-hour estimated. In the later years the oblique hauls were each of one half-hour's duration. In both cases these half-hour catches have been added together for each month in the year and divided by the number of catches per month. In this way an average monthly catch for each year was obtained (Table 3). By adding the averages for any one month and dividing by the number of years in which collections were made in that month, an average monthly catch was obtained for the period of six years covered by the researches (Table 1, p. 712). In Table 2 (p. 717) are given the dates in each year when collections were made, and it can be seen that although the winter months have been very poorly represented the important period of April to September has been fairly well covered.

Figure 1 shows the average monthly catches (as given in Table 1) for

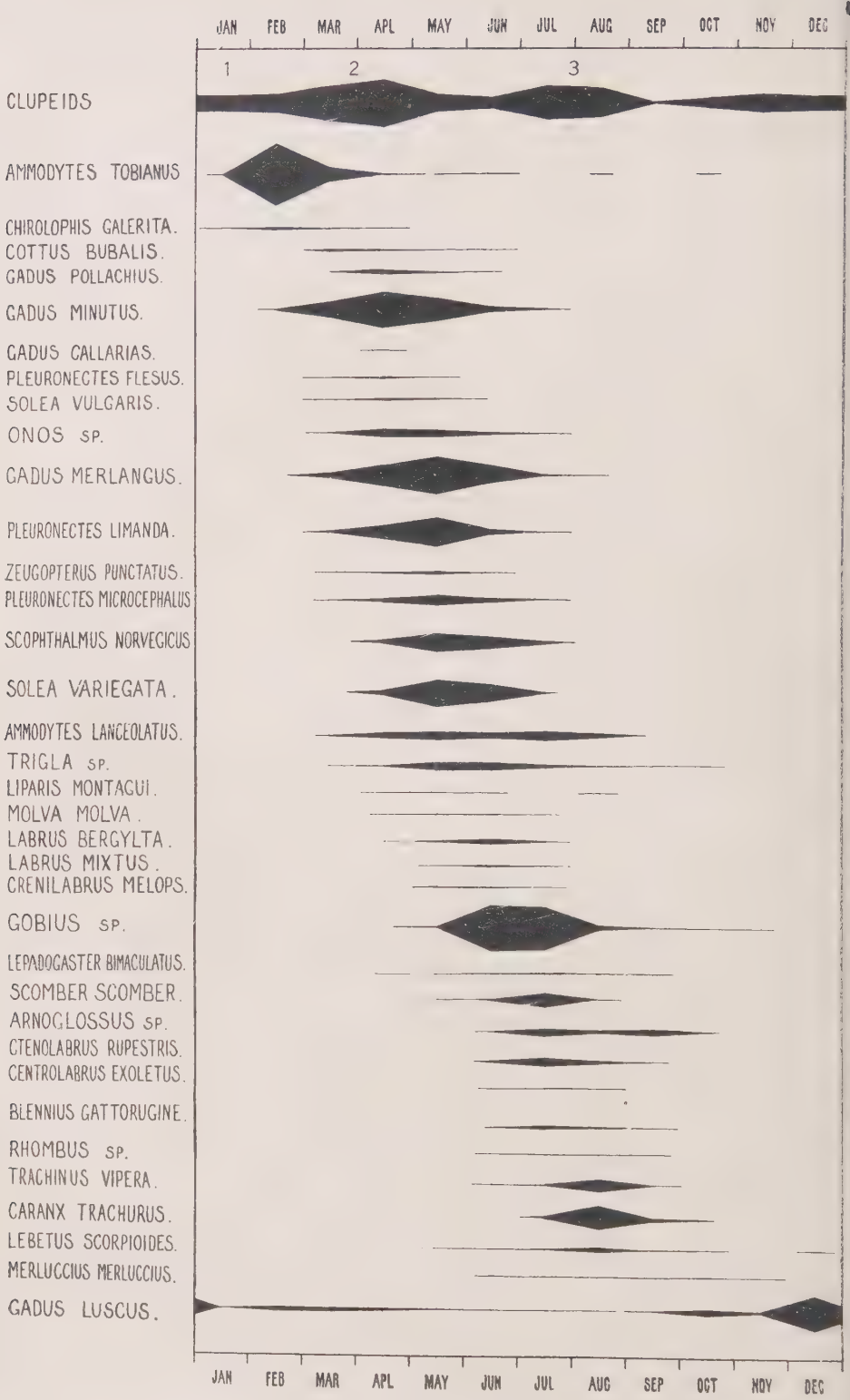

FIG. 1 (description opposite).

each species in graphic form. The abundance curves for each species are drawn to the same scale so that from this figure one can see at a glance the comparative abundance of the post-larvæ of any species of fish at

FIG. 2.—Diagram to show in graphic form the seasonal distribution and abundance of the post-larvæ of Callionymus sp., mostly *C. lyra*, in offshore waters off Plymouth. This figure is drawn to the same scale as Figure 1, and shows the marked superiority in the numbers of post-larvæ of this species over all other species, excepting perhaps the Gobies.

any time of the year. (This figure shows only those species whose average number for any month is one per half-hour's haul or more.)

In this publication only those observations made at the International Hydrographic Stations L4 and L6, or at the station two miles east of the Eddystone have been included, and from 1926 onwards practically all the collections were made from the latter position. The results are therefore indicative of the general offshore conditions. They should, if possible, be supplemented by a series of collections quite close inshore when possibly certain species, such perhaps as the wrasses, might appear more abundant.

DESCRIPTION OF FIGURE 1.

FIG. 1.—Diagram to show in a graphic form the results expressed in Table 1. The blackened areas indicate the time of year at which post-larval stages of each species may be expected in the ring-trawl catches in offshore waters off Plymouth; each area is drawn to the same scale and indicates the comparative abundance of the post-larvæ of each species as averaged over the years 1924 to 1929. Only those species whose post-larvæ appear with an average of over one specimen per half-hour's haul are shown here. In the case of the Clupeids the Figures 1, 2 and 3 indicate the periods when the catches may be expected to consist almost entirely of Herrings, Sprats, or Pilchards respectively.

N.B. The results for Gobies should probably be very much larger, these post-larvæ being generally near the bottom in the daytime and below the region sampled by the ring-trawl; the same also may hold for *Gadus minutus*.

A glance at Figure 1 shows how few species compared with the large number occurring in the area can be considered as abundant. The outstanding feature as shown in Figure 2 (drawn to the same scale as Figure 1) is the abundance of Callionymus sp. post-larvae probably mostly *C. lyra*. Ever since researches into the young stages of our fish were first systematically undertaken by Clark (1910) the abundance of this species has been noticeable.

Although the ring-trawl collections do not show the post-larval gobies to have been especially numerous it is quite possible that they are actually even more abundant than those of Callionymus. Catches with the bottom plankton net have shown that they are present in great numbers in the daytime near the bottom, and in 1927 the average catches for June and July respectively were 1354 and 3247 as against 2·1 and 2·1 in collections made by the ring-trawl fished obliquely ; this is many times more numerous than Callionymus.

It is thought that these average figures will form a good basis to work on in watching for any violent fluctuations in the future. They are presented here only as data, because until such observations have covered a long period of years it will not be known how great the differences from year to year must be before they can be regarded as significant.

There is an indication that the post-larval stages of certain spring spawners were but poorly represented in the year 1929, as for example, *Gadus minutus*, *Pleuronectes microcephalus*, *Solea variegata*, and Callionymus sp. Such differences will naturally tend to lower the averages given in Table 1. Similarly the year 1926 seems to have been marked by a rather unusual abundance of young mackerel, *Scomber scomber ;* never in all the past records given by Clark (1914 and 1920) and Allen (1917) have so many been caught. This may perhaps have meant an easterly extension of their normal spawning-grounds, the abundance of the copepod, *Calanus finmarchicus*, being very great in this region that summer and hence perhaps the adults moving more in this direction. At any rate there is no indication from commercial catches that 1926 was an exceptionally good survival year, as they should probably have been appearing in the catches by now (1929).

The above instances have been cited to emphasize that we do not yet know what differences to look for as being significant. The results of the research on the vertical distribution of the post-larval fishes have shown that for the majority of species oblique daytime hauls with the net fished as deep as possible should give a fair picture of the quantities of young fish present (Russell, 1928, p. 833). In the case of post-larval Clupeids, however, these results do not give a correct impression (Russell, 1930 p. 649), although if they were unusually abundant any one year their increased numbers would perhaps show up in the daytime as well as at

night. In the case of the Gobies, and also possibly *Gadus minutus* (Russell, 1930, p. 650), the hauls probably have not gone deep enough to sample the zone of their maximum abundance.

A comparison of these results with the figures given by Allen (1917) shows that there have not been any marked changes in the composition of the catches since that date, and his averages for the years up to 1914 agree well with those given here. As regards the sizes of the post-larvæ caught, there will be some slight difference for each species as the season advances. When first any species starts to appear in the catches it is natural that the majority should be very young forms, and while a few of the smallest sizes are usually to be taken throughout the season there will be a gradual increase in size of the majority as time goes on, until in the last catches in which they appear the post-larvæ will mostly be in the neighbourhood of the size at which they disappear from the ring-trawl catches either owing to their leaving the plankton or having become strong enough swimmers to evade the net. In Table 3 are given for the commoner species the sizes within which the majority of post-larvæ taken in the ring-trawl lie; larger sizes will of course be caught at times in the case of all species.

A bibliography is given here including all those papers that have been published dealing with the post-larval stages of Teleostean fishes in the Plymouth area (see pp. 720–722).

The months in which the maximum abundance of the post-larvæ of each species may be expected are given below.

MONTHS OF AVERAGE MAXIMAL ABUNDANCE OF POST-LARVÆ.

January.	February.	March.	April.
	C. harengus	*C. bubalis*	*C. sprattus*
	A. tobianus	*A. cataphractus*	*G. pollachius*
	C. galerita		*G. minutus*
			G. callarias
			P. flesus
			S. vulgaris
			Onos sp.

May.	June.	July.	August.
G. merlangus	*M. molva*	*C. pilchardus*	*Zeus faber*
P. limanda	Callionymus sp.	*R. raninus*	Rhombus sp.
Z. punctatus	*L. bergylta*	*Capros aper*	*S. cabrilla*
P. microcephalus	*L. mixtus*	*S. scomber*	*T. vipera*
S. norvegicus	*C. melops*	Arnoglossus sp.	*C. trachurus*
S. variegata	Gobius sp.	*S. lascaris*	*M. surmuletus*
Trigla sp.		*S. lutea*	*C. rubescens*
L. montagui		*A. lanceolatus*	*L. scorpioides*
		C. rupestris	*B. ocellaris*
		C. exoletus	
		B. pholis	
		B. gattorugine	
		L. piscatorius	
		L. bimaculatus	

September.	October.	November.	December.
—	*M. merluccus*	—	*G. luscus*

TABLE 1.

AVERAGE MONTHLY CATCHES OF POST-LARVÆ PER HALF-HOUR HAUL WITH 2-METRE RING-TRAWL FISHING AT ALL DEPTHS, 1924–1929.

	Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Clupeid sp.*	23·7	30·3	51·6	70·7	25·0	15·5	48·4	42·6	1·6	16·6	30·0	22·5
Gadus pollachius	–	–	1·2	7·7	1·6	0·1	–	–	–	–	–	–
G. merlangus	–	–	7·8	32·0	55·9	32·8	2·3	0·2	–	–	–	–
G. minutus†	–	3·9	24 0	52·5	33·6	8·8	0·9	–	–	–	–	–
G. luscus	0·9	6·9	5·4	3·8	1·8	0·8	0·1	1·4	0·7	7·1	3·9	49·5
G. callarias	–	–	–	1·1	–	–	–	–		–	–	–
Onos sp.	–	–	0·6	14·8	10·4	3·3	0·8	–	–	–	–	–
Molva molva		–	–	0·1	3·5	4·6	0·1	–	–	–	–	–
Merluccius merluccius			–		–	0·3	0·2	0·2	0·2	1·6	0·9	–
Raniceps raninus					–	0·04	0·2	0·2	–	0·1	–	
Capros aper	–	–		–	–	0·04	0·3	0·3	0·1	–	–	–
Zeus faber	–	–		–		–	–	0·1	–	–	–	–
Arnoglossus sp.			–		–	0·2	12·4	7·6	10·5	2·0		
Rhombus sp.	–			–	–	0·2	1·8	2·4	0·6	–	–	–
Scophthalmus norvegicus	–	–		5·8	29·8	18·3	6·4	–	–	–		–
S. unimaculatus	–		–	–	+	+	+	–	–	–	–	–
Zeugopterus punctatus	–	–	0·6	1·2	6·2	0·8	–	–		–	–	–
Pleuronectes limanda	–	–	6·6	21·8	45·3	8·8	0·2	–	–	–	–	–
P. flesus	–	–	0·3	4·5	0·7	–	–	–		–	–	–
P. microcephalus	–	–	0·3	6·3	16·1	8·4	1·5	–	–	–	–	–
Solea vulgaris	–	–	0·3	4·9	1·0	0·04	–			–	–	–
S. variegata	–	–	–	5·8	40·5	29·1	3·4		–	–	–	–
S. lascaris	–		–		–		0·1	–		0·4	–	–
S. lutea	–	–	–	–		–	0·1	–	–	–	–	–
Serranus cabrilla	–						–	0·3	0·1	0·2	–	–
Caranx trachurus					–		3·9	34·4	3·6	2·0	–	–
Mullus surmuletus	–		–	–	–	–	–	0·1	–	–	–	–
Ammodytes tobianus	0·6	90·9	20·7	2·6	0·1	0·2	–	0·2	0·4	0·2	–	–
A. lanceolatus			2·4	8·6	13·9	9·1	14·8	8·1		–	–	–
Cepola rubescens	–				–	0·04	0·1	0·4		–	–	

Callionymus sp.	–	–	8·7	89·0	377·6	395·0	59·2	24·1	1·1	9·6	0·9	–
Labrus bergylta	–	–	–	0·1	1·3	9·1	1·2	–	–	–	–	–
L. mixtus	–	–	–	–	0·2	5·9	1·4	–	–	–	–	–
Ctenolabrus rupestris	–	–	–	–	–	2·5	12·0	4·9	0·1	–	–	–
Crenilabrus melops	–	–	–	–	–	2·9	2·5	0·7	–	–	–	–
Centrolabrus exoletus	–	–	–	–	–	1·3	1·9	0·8	–	–	–	–
Trachinus vipera	–	–	–	–	–	0·4	2·6	18·3	1·0	–	–	–
Trachinus draco	–	–	–	–	–	–	–	–	0·1	–	–	–
Scomber scomber ‡	–	–	–	–	0·1	5·8	22·8	0·2	–	–	–	–
Gobius sp.§	–	–	–	0·9	1·8	68·8	62·9	8·0	1·2	0·5	0·9	–
Lebetus scorpioides	–	–	–	–	0·2	0·7	2·7	8·7	1·5	0·3	–	2·1
Blennius ocellaris	–	–	–	–	–	0·2	0·4	0·8	–	–	–	–
B. pholis	–	–	–	–	0·1	0·8	0·8	0·2	–	–	–	–
B. gattorugine	–	–	–	–	–	2·5	6·4	5·2	0·3	–	–	–
Chirolophis galerita	0·3	3·0	2·0	0·3	–	–	–	–	–	–	–	–
Trigla sp.¶	–	–	1·5	3·0	13·4	12·5	5·5	3·5	0·7	0·9	–	–
Cottus bubalis	–	–	4·5	2·6	0·7	0·5	–	–	–	–	–	–
Agonus cataphractus	–	–	0·3	0·1	0·1	–	–	–	–	–	–	–
Liparis montagui	–	–	–	0·3	1·1	0·8	–	0·3	–	–	–	–
Lepadogaster bimaculatus	–	–	–	0·3	0·1	2·4	1·6	1·3	0·3	–	–	–
Lophius piscatorius	–	–	0·3	0·04	–	0·3	0·8	0·1	–	–	–	–
Belone vulgaris+	–	–	–	–	–	–	–	–	0·1	–	–	–

* Includes *Clupea harengus*, *Clupea sprattus*, and *Sardina pilchardus*. Post-larval herring occur mostly in January, February, and March; sprat in March, April, and May, the increase being generally due to larger numbers of recently hatched sprat: from May till end of year the catches are mostly pilchard which spawn intermittently throughout the summer.

† *Gadus minutus* post-larvæ live normally very deep in the water in the daytime, and possibly these averages should be considerably higher to give a true picture.

‡ In calculating these averages for *Scomber scomber*, the mackerel, the results for 1926 have not been included as it is thought that perhaps this may have been an abnormal year (see Table 3).

§ The post-larval gobies live very near the bottom in the daytime, and these averages should probably be very much higher.

¶ Consist of *Trigla gurnardus*, *T. cuculus*, and *T. hirundo* chiefly.

\+ Less than 0·1.

TABLE 2.

DATES ON WHICH COLLECTIONS WERE MADE.

	1924	1925	1926	1927	1928	1929	Total days.
January	—	—	—	—	9th 16th 26th 30th	—	4
February	—	—	—	-	2nd 20th 27th	—	3
March	—	—	—		5th 21st 30th	—	3
April	—	2nd 8th 29th	9th 13th (i) 13th (ii) 22nd 26th	4th 14th 26th	4th 11th 12th 23rd	10th 19th 23rd 29th	19
May	29th	19th (i) 19th (ii)	6th 19th	2nd 9th 16th 25th	—	6th 13th 23rd 27th	13
June	25th	4th (i) 4th (ii) 17th 18th 19th	3rd 4th 25th 30th	2nd 9th 29th		6th 11th 25th	16
July	1st 15th 16th	1st (i) 1st (ii) 16th 29th	6th 13th 26th	8th 12th 21st 26th	—	3rd 9th 18th 23rd 30th	19
August	—	6th	4th	4th 8th 19th 26th 31st	—	9th 15th 22nd 26th	11
September	—	—	22nd	6th 15th 19th	—	4th 6th 10th 17th 24th	9
October	—	—	—	4th 13th 18th 24th	—	3rd 10th 16th	7
November	—	—	—	1st	—	—	1
December	—	—	—	15th 21st	—	—	2

TABLE 3.

Average Monthly Catch of Post-larvæ per 30-minute Haul with Ring-trawl.

		Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Clupeid sp.	1924					42·0	28·5	67·2					
Herring	1925				47·7	10·8	9·2	6·6	0·9				
Sprat	1926				95·4	57·9	15·9	63·0	150·0	1·2			
Pilchard	1927				107·4	7·8	8·1	81·3	14·1	1·2	2·4	30·0	22·5
5–20 mm.	1928	23·7	30·3	51·6	82·5								
	1929				20·7	6·3	15·9	24·0	5·4	2·4	30·7		
Gadus pollachius	1924					–		–					
Pollach	1925				10·5	0·3	0·1						
4·5–12 mm.	1926				3·3	5·7	0·3	–	–				
	1927				0·9	1·2	–						–
	1928	–		1·2	21·6								
	1929				2·4	0·6			–				
Gadus merlangus	1924					42·0	80·4	2·1					
Whiting	1925				31·2	83·1	23·7	4·5	–				
4–12 mm.	1926				52·5	55·8	36·6	0·9	0·6	–			
	1927				14·4	51·0	8·4	0·6	0·2	–		–	
	1928			7·8	29·7								
	1929				32·4	47·7	15·0	3·6	–				
Gadus minutus	1924					33·9	24·9	4·2					
Poor Cod or Bib	1925				42·9	49·8	4·8	–					
4–12 mm.	1926				56·1	40·2	12·9						
	1927				17·4	43·2	–					–	–
	1928	–	3·9	24·0	135·6								
	1929				10·5	0·9	1·2	0·3					
Gadus luscus	1924					3·0	1·5						
Pouting or Pout	1925				2·1	–	0·1	0·2	–				
4–10 mm.	1926				3·9	3·6	1·8	–	2·4				
	1927				1·5	2·4	0·3	–	0·6	0·3	2·1	3·9	49·5
	1928	0·9	6·9	5·4	8·4								
	1929				3·0	–	0·3	0·3	2·1	1·8	12·0		
Gadus callarias	1924												
Cod	1925						–						
4–10 mm.	1926				2·1			–	–				
	1927					–					–		–
	1928				0·3								
	1929				3·3				–	–			
Onos sp.	1924					15·0	3·0	3·0					
Rockling	1925				24·3	8·4	0·9						
4–10 mm.	1926				17·1	23·7	7·2	–	–	–			
	1927				0·3	3·9	0·9			–		–	–
	1928	–	–	0·6	31·8								
	1929				0·3	0·9	4·5	0·9	–	–	–		
Molva molva	1924					9·9	9·9	–					
Ling	1925				–	0·9	0·6	0·6	–				
5–14 mm.	1926				0·1	4·8	12·3	–	–	–			
	1927				–	1·5	–	–	–				–
	1928	–	–	–	0·3								
	1929				–	0·3			–		–		
Merluccius	1924					–	1·5	–					
merluccius	1925				–		–	–	–				
Hake	1926					–	0·2	0·9	–				
5–10 mm.	1927				–	–	–	0·2	0·6	–	1·5	0·9	–
	1928	–	–	–	–								
	1929					–	–	–	0·3	0·6	1·7		
Raniceps raninus	1924							–					
Lesser Forkbeard	1925						–	0·2	0·6				
4–6 mm.	1926				–	–	0·2	0·6	–	–			
	1927						–	0·2	0·2	–	0·3	–	–
	1928	–	–	–									
	1929				–	–	–	0·2	–		–		

		Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Capros aper	1924					–	0·2	–					
Boar-fish	1925				–	–	–	–	–				
3–6 mm.	1926				–		–	·	0·5	–			
	1927				–	–		0·8	–		–	–	–
	1928	–	–	–	–								
	1929				–	–		–	0·5	0·3			
Zeus faber	Only caught August, 1926. Average 0·5.												
John Dory													
Arnoglossus sp.	1924					–	0·9	4·2					
Scaldbacks	1925				–		–	4·8	4·5				
4–20 mm.	1926				–		0·1	18·3	9·9	16·8			
	1927				–	–	·	15·0	7·2	3·0	0·9	·	
	1928	–	–	–	–								
	1929				–	–	–	19·5	8·7	11·7	3·0		
Rhombus sp.	1924					–	0·8	–					
Turbot and Brill	1925				–	–	–	–	–				
4–10 mm.	1926				–	–	0·1	3·2	8·6	0·6			
	1927				–	–	–	3·3	0·8	0·6	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	2·4	0·3	0·6	–		
Scophthalmus	1924					32·1	20·4	17·4					
norvegicus	1925				22·5	92·1	13·8	2·4					
Norway Topknot	1926				0·9	15·3	42·6	1·8	·	–			
4–10 mm.	1927				0·9	8·7	3·6	0·9	–	–	–	–	–
	1928	–	–	–	4·8								
	1929				–	0·6	11·1	9·3	–	–	–		
S. unimaculatus	Only 6 caught during the 6 years. E1 17/6/24, 2 ; A, 1/7/25, 1 ; 7/5/24, 1 ; 17–18/7/25, 2 (dusk and dark).												
Zeugopterus	1924					11·1	–	–					
punctatus	1925				1·8	12·6	0·2	–	–				
Topknot	1926				0·9	2·7	3·6	–	–	–			
4–10 mm.	1927				1·2	4·2	–	–	–	–	–	–	–
	1928	–	–	0·6	2·1								
	1929				–	0·6	–	–	–	–	–		
Pleuronectes	1924					24·0	15·9	0·9					
limanda	1925				26·4	69·6	3·9	0·3	·				
Dab	1926				24·3	50·1	9·3	–	–	–			
5–12 mm.	1927				6·6	68·4	2·1	–	–	–	–	–	–
	1928	–	–	6·6	37·2								
	1929				14·7	14·4	12·6	–	–	–	–		
Pleuronectes flesus	1924					–	–	–					
Flounder	1925				1·2	2·7	–	–	–				
4–9 mm.	1926				6·0	0·6	–	–	–	–			
	1927				3·9	0·2	–	–	–	–	–	–	–
	1928	–	–	0·3	10·8								
	1929				0·6	·	–	–	–	–	–		
Pleuronectes	1924					21·9	21·6	4·5					
microcephalus	1925				8·7	24·6	3·9	0·9	–				
Merrysole or	1926				3·6	27·6	13·2	1·2	–	–			
Lemon Dab	1927				1·5	6·0	0·6	–	–	–	–	–	–
4–13 mm.	1928	–	–	0·3	17·7								
	1929				–	0·6	2·7	0·9	–	–	–		
Solea vulgaris	1924					–	–	–					
Common Sole	1925				2·4	1·2	–	–	–				
4–9 mm.	1926				6·0	1·8	0·2	–	–	–			
	1927				6·3	1·2	–	–	–	–	–	–	–
	1928	–	–	0·3	3·3								
	1929				6·3	0·6	–	–	–	–	–		
Solea variegata	1924					20·1	111·0	6·1					
Thickback	1925				9·9	101·4	6·3	0·9	–				
4–11 mm.	1926				5·7	49·8	25·5	3·9	–	–			
	1927				2·1	29·4	0·3	3·6	–	–	–	–	–
	1928	–	–	–	10·2								
	1929				0·9	1·8	2·4	2·7	–	–	–		
Solea lascaris	1924					–	–	–					
Sand Sole	1925				–	–	–	–	–				
	1926				–		–	–	–	–			
	1927				–	–	–	0·3	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	·	–	0·4	–	–	0·7		

		Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Solea lutea	1924					–	–	–					
Solenette	1925				–	–	–	–	–				
	1926				–	–	–	–	–	–			
	1927				–	–	–	–	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	0·6	–	–	–		
Serranus cabrilla	1924					–	–	–					
Sea Perch	1925				–	–	–	–	–				
	1926				–	–	–	–	1·0	0·3			
	1927				–	–	–	–	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	–	–	–	0·3	–	–
Caranx trachurus	1924					–	–	6·3					
Horse Mackerel	1925				–	–	–	–	–				
or Scad	1926				–	–	–	1·8	107·1	4·5			
4–15 mm.	1927				–	–	–	9·9	9·3	0·3	0·3	–	–
	1928	–	–	–	–								
	1929				–	–	–	0·6	21·3	5·7	3·7		
Mullus surmuletus	1924					–	–	–					
Red Mullet	1925				–	–	–	–	–				
	1926				–	–	–	–	–	–			
	1927				–	–	–	–	0·4	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	–	–	–	–		
Ammodytes tobianus	1924					–	–	–					
Lesser Sandeel	1925				0·2	–	0·1	–	–				
4–20 mm.	1926				2·4	0·3	0·5	–	–	1·2			
	1927				7·8		0·3	–	0·6	–	–	–	–
	1928	0·6	90·9	20·7	0·9								
	1929				1·5	–	–	–	0·3	–	0·3		–
Ammodytes	1924					12·0	16·5	35·1					
lanceolatus	1925				11·1	37·5	7·5	18·9	5·1				
Greater Sandeel	1926				1·5	12·6	10·8	13·5	22·5	–			
5–20 mm.	1927				8·7	6·9	5·4	3·6	0·9	–		–	–
	1928	–	–	2·4	21·0								
	1929				0·9	0·6	5·1	2·7	3·9	–	–		
Cepola rubescens	1924					–	–	–					
Red Band Fish	1925				–	–	–	–	–				
	1926				–	–	–	0·2	–	–			
	1927				–	–	–	–	–	0·7	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	–	0·5	–	–		
Callionymus sp.	1924					347·1	1102·5	95·1					
Dragonets	1925				55·8	442·8	144·9	80·7	3·6				
3–8 mm.	1926				99·6	507·6	648·0	39·3	70·5	–			
	1927				24·0	533·7	24·3	11·4	7·8	1·8	18·9	0·9	–
	1928	–	–	8·7	212·1								
	1929				53·4	57·0	55·2	69·3	14·4	1·5	0·3		
Labrus bergylta	1924					0·9	24·0	4·5					
Ballan Wrasse	1925				0·2	1·8	1·2	0·3	–				
4–9 mm.	1926				0·2	3·0	12·6	0·2	–	–			
	1927				–	0·6	6·9	–	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	0·6	1·2	–	–	–		
Labrus mixtus	1924					–	22·5	5·4					
Cuckoo Wrasse	1925				–	0·3	0·2	–	–				
4–9 mm.	1926				–	0·6	6·0	1·2	–	–			
	1927				–	–	0·9	–	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	0·6	–	–	–		
Ctenolabrus rupestris	1924					–	1·5	5·7					
	1925				–	–	0·3	1·2	0·6				
4–9 mm.	1926				–	–	9·9	39·6	8·4	–			
	1927				–	–	0·6	6·0	4·5	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	7·5	6·0	0·3	–		
Crenilabrus melops	1924					–	6·6	11·7					
	1925				–	–	–	0·3	2·4				
4–7 mm.	1926				–	–	5·4	0·3	–	–			
	1927				–	–	2·4	–	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	–	0·3	–	–		

		Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Centrolabrus exoletus 4·7 mm.	1924					–	0·9	5·7					
	1925				–	–	0·1	0·6	2·4				
	1926				–	–	1·8	2·1	–	–			
	1927				–	–	3·0	0·2	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	0·6	0·9	0·6	–	–		
Trachinus vipera Lesser Weever 3–11 mm.	1924					–	–	0·6					
	1925				–	–	–	3·3	3·6				
	1926				–	–	0·6	4·2	57·0	–			
	1927				–	–	1·2	2·4	3·9	0·3	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	2·4	8·7	2·7	–		
Trachinus draco Greater Weever	1924					–	–	–					
	1925				–	–	–	–	–				
	1926				–	–	–	–		–			
	1927				–	–	–	–	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	·	–	0·2	–		
Scomber scomber Mackerel 4–12 mm.	1924					–	15·0	8·1					
	1925				–	–	6·0	2·4	–				
	1926				–	–	18·9	178·5	146·4	–			
	1927				–	0·6	1·2	23·4	0·9	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	1·2	57·3	–		–		
Gobius sp. Gobies 3–10 mm.	1924					6·9	278·4	170·4					
	1925				–	0·3	5·7	12·9	11·4				
	1926				2·1	·	41·4	68·1	5·4	–			
	1927				0·3	0·9	2·1	2·1	6·0	0·9	0·6	0·9	–
	1928	–	–	–	2·1								
	1929				–		16·2	60·9	9·3	2·7	0·3		
Lebetus scorpioides 3–6 mm.	1924					·	0·9	0·9					
	1925				–	–	0·1	0·9	5·1				
	1926				–	0·9	2·4	8·4	25·5	1·8			
	1927				–	0·2	0·3	1·2	1·5	0·3	0·3	–	2·1
	1928	–	–	–	–								
	1929				–	–	–	2·1	2·7	2·4	0·3		
Blennius ocellaris Butterfly Blenny	1924					–	0·9	0·6					
	1925				–	–	–	0·2	1·5				
	1926				–	–	–	1·2	0·9	–			
	1927				–	–	–	–	0·6	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	–	–	–	–		
Blennius pholis Shanny	1924					–	0·9	1·2					
	1925				–	0·3	0·2	1·2	0·6				
	1926				–	–	2·4	0·9	–	–			
	1927				–	0·2	0·3	0·9	0·2	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	–	–	–	–		
Blennius gattorugine Tompot 5–10 mm.	1924					–	3·6	6·0					
	1925				–	–	0·9	5·4	2·1				
	1926				–	–	7·2	12·6	8·4	–			
	1927				–	–	0·9	2·1	3·6	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	5·7	6·6	0·9	–		
Chirolophis galerita Yarrell's Blenny 4–7 mm.	1924					–	–	–					
	1925				0·6	–	–	–	–				
	1926				–	–	–	–	–	–			
	1927				–	–	–	–	–	–	–	–	–
	1928	0·3	3·0	2·0	–								
	1929				0·8	–	–	–	–	–	–		
Agonus cataphractus Pogge	1924					–	–	–					
	1925	·			–	–	–	–	–				
	1926				–	–	–	–	–	–			
	1927				–	–	–	–	–	–	–	–	–
	1928	–	–	0·3	0·3								
	1929				0·3	0·3	–	–	–	–	–		
Trigla sp. Grey and Red Gurnards, and Tub 4–12 mm.	1924					9·9	45·0	9·9					
	1925				1·5	38·4	3·3	5·4	0·6				
	1926				6·0	5·7	7·8	2·4	5·1	0·6			
	1927				–	7·5	3·9	6·0	1·5	–	–	–	–
	1928	–	–	1·5	0·3								
	1929				7·2	5·7	2·7	3·6	6·6	1·5	1·7		

		Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Cottus bubalis	1924					0·9	1·5	–					
Father Lasher	1925				0·3	0·6	0·1	–					
5–8 mm.	1926				1·5	–	0·3	–	–	–			
	1927				1·5	0·9	–	–	–	–	–	–	–
	1928	–	–	4·5	6·0								
	1929				3·6	0·9	0·6	–	–	–	–		
Liparis montagui	1924					–	3·6	–					
Montague's Sucker	1925				0·2	1·2	–	–	1·0				
7–10 mm.	1926				0·3	–	–	–	–				
	1927				–	3·0	–	–	–	–	–	–	–
	1928	–	–	–	0·8								
	1929				0·3	–	0·3	–	–	–	–		
Lepadogaster	1924					–	7·5	3·6					
bimaculatus	1925				–	0·3	0·2	1·5	0·9				
Doubly Spotted	1926				–	0·3	2·4	0·6	2·1	–			
Sucker	1927				1·5	–	–	–	0·2	–	–	–	–
5–10 mm.	1928	–	–	–	–								
	1929				–	–	2·1	2·1	2·1	0·9	–		
Lophius piscatorius	1924					–	–	1·5					
Angler	1925				–	–	–	–	–				
5–9 mm.	1926				0·2	–	0·6	1·8	–	–			
	1927				–	–	0·3	0·3	0·2	–	–	–	–
	1928	–	–	0·3	–								
	1929				–	–	0·6	0·3	–	–	–		
Belone vulgaris	1924					–	–	–					
Garfish	1925				–	–	–	–	–				
	1926				–	–	–	–	–	–			
	1927				–	–	–	–	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	–	–	0·2			

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Herring Investigations at Plymouth. VIII. The Transition from Larva to Adolescent.

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With 12 Figures in the Text.

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Introduction.

Investigations concerning the main events in the transformation of the transparent eel-shaped larval herring into the silvery and scaled adolescent fish may proceed along two lines. In the first place, information may be sought as to the biological processes which bring about each event. For example, attention may be directed to the study of the differential growth of the body by which the form of the adult is attained; or, to the manner in which the scales are developed. But, secondly, it is of vital importance to learn how much the events of metamorphosis are affected by circumstances of time and place. Thus, at Plymouth, as elsewhere, we need to know the extent of possible differences in form and size between young fishes which have metamorphosed from larvæ born at different times.

Sufficient material has been collected from the rivers flowing into the sea at Plymouth to yield information along both the above lines of investigation. In the first section of this paper attention is given to the

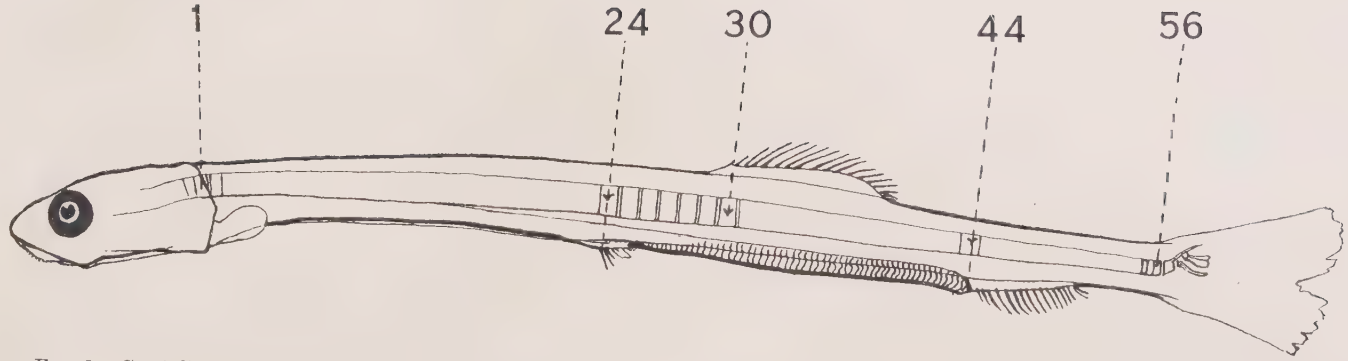


FIG. 1.—Semi-diagrammatic drawing of post-larval herring. Body-length (L_B) of 33 mm. Position of pelvics, first dorsal ray and anus with respect to vertebræ. Total number of vertebræ is 56, exclusive of compound urostyle.

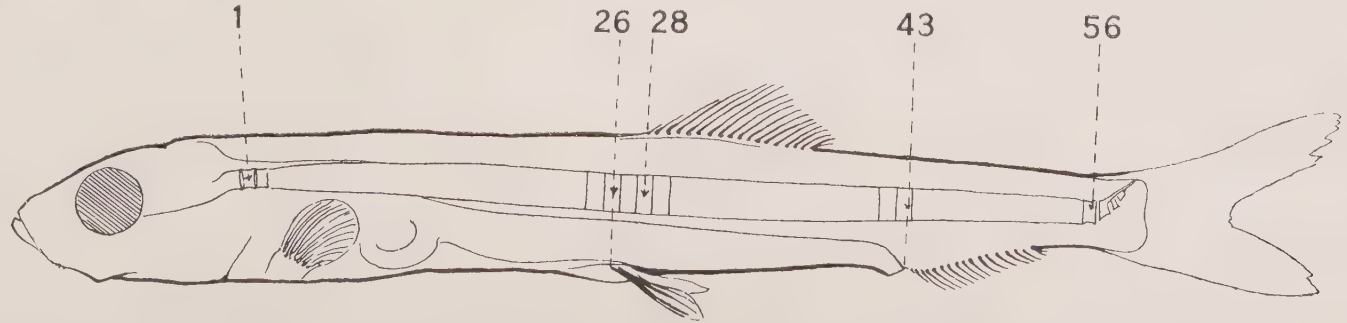


FIG. 2.—Post-larval herring; body-length (L_B) of 36 mm. Note apparent movement of pelvics, dorsal fin and anus with respect to vertebræ.

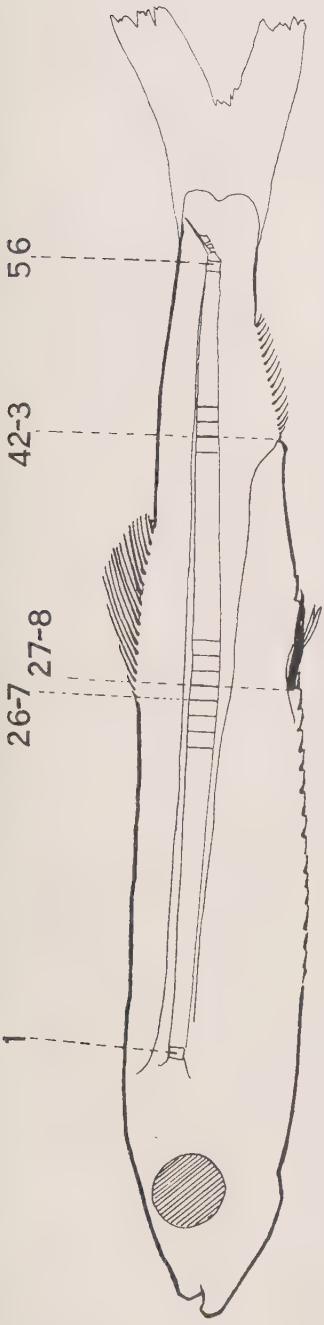


FIG. 3.—Post-larval herring; body-length (L_B) of 37 mm. Pelvics now lie slightly farther back than first dorsal ray with respect to vertebræ. Anus has moved still farther forward.

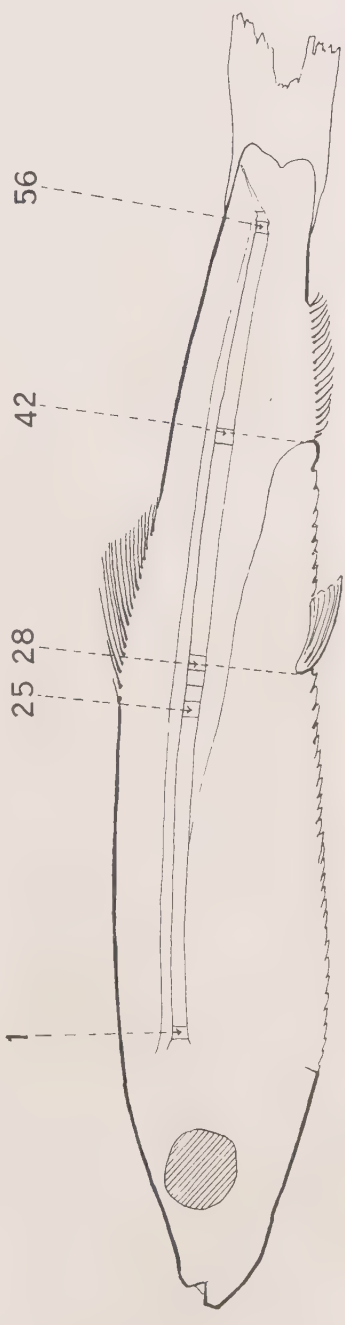


FIG. 4.—Post-larval herring; body-length (l_B) 45 mm. Pelvics well behind first dorsal ray, and anus beneath vertebra 42.

question of the differential growth of the body, while in the second, problems arising out of observed differences between samples of metamorphosing fishes are discussed.

Collection of Data.

The fishes studied were caught in a small-meshed Saltash tuck-seine in the Rivers Tamar and Lynher [charts of the district are given by Ford (**3**) and Percival (**6**)]. As a measure of length, the body-length L_B from the tip of the snout to the end of the caudal peduncle, was used in preference to the more familiar total-length L_T, for reasons previously stated in Ford (**3**, p. 307). The value of L_T is approximately equal to 7/6 L_B. The method of statistical "grouping" was also the same as that hitherto used; e.g. fishes from 30 to 34 mm. would be grouped in the 30 mm. group, and those from 35 to 39 mm. in the 35 mm. group, when grouping was by intervals of 5 mm. For the first part of the work, fifty specimens of each of the four body-length groups 30 mm., 35 mm., 40 mm., and 45 mm. from any one day's sample were utilised. These were stained in alizarin either whole, or after the excision of one side by means of a safety-razor blade, and then cleared in xylol. A count of the total number of vertebræ in each specimen was made, and the position, either immediately above or below a particular vertebra, of the first dorsal fin-ray, the pelvics and the anus noted. The count of the total number of vertebræ stopped at the vertebra immediately preceding the compound urostyle (*vide* Ford, **2**, p. 253). In determining the relative position of the fins and anus, it frequently happened that the structure concerned occupied a position opposite the interval between two adjacent vertebræ. In such cases an entry of $\frac{1}{2}$ was made to each of the appropriate vertebræ classes. At a later stage in the work, actual measurements along the body to determine well-defined body intervals were made on specimens prior to staining.

CHANGE OF FORM.

Alteration in Position of Fins and Anus Relative to Vertebræ.

Fage (**1**) and Lebour (**5**) have shown that in the gradual adjustment of the fins and anus of the larva to the positions they occupy in the adult, these structures alter their place with respect to the vertebræ.* Thus

* Since this paper has been in the hands of the printer, the important work by Dr. Schnakenbeck on the development of the herring has appeared. (*Entwicklungsgeschichtliche und morphologische Untersuchungen am Hering.* Berichte d. Deutsch. wissenschaftl. Komm. f. Meeresforschung, Neue Folge, Band V Heft 2, Berlin, 1929.) Dr. Schnakenbeck has studied the process of metamorphosis in relation to the growth of the myotomes. Excellent illustrations are given.

there is a relative movement forward of the dorsal fin and anus, but a backward one of the pelvics. In order to assist those readers who may not be familiar with these facts, Figures 1, 2, 3, and 4 have been inserted. But as individual fishes differ in their total number of vertebræ from 53 to 58, it is clearly of importance to study the effect of this difference in total with regard to the relative movements of fins and anus. For example, the 25th vertebra, under which the pelvics may lie in a fish having a total of 55 vertebræ, is not in the same relative position along the vertebral column as the 25th vertebra of a second fish having 57 vertebræ. Hence, in analysing the progress of development over a range of time or size, it is necessary to take into account the total number of vertebræ of the individuals concerned.

Fishes with 56 Vertebræ.

It is convenient to commence with those fishes which form the greater proportion of each sample taken, namely, those with a total of 56 vertebræ. Data are available for a total of 746 such fishes caught during the months of April, May and June, and varying in body-length from 30 to 49 mm. The position of the pelvics in these specimens varies from beneath the 24th vertebra to beneath the 29th. The variation in position of the first dorsal ray (D^1) when the pelvics lie under the 24th, 25th to the 29th vertebra respectively is given in the following table :—

TABLE I.

Position of Pelvics. No. of specimens in which pelvics lie beneath vertebræ as under.	Position of 1st Dorsal Ray (D^1). No. of Specimens in which D^1 lies above vertebra as under								Totals.	Position of D^1 Working means.
	24	25	26	27	28	29	30	31		
24	–	–	–	–	–	–	2	–	2	29·5*
24–25	–	–	–	–	½	3	6½	3	13	29·42
25	–	–	–	1	3½	23½	33	9	70	29·15
25–26	–	–	–	1½	2	13½	6	5	28	28·89
26	–	–	8½	16½	37½	46	29	2½	140	28·06
26–27	–	1	8	10	16½	8	½	–	44	27·05
27	2½	26	60½	57½	20	3½	1	–	171	25·97
27–28	1	25½	19½	5½	3½	–	–	–	55	25·23
28	3½	75	90	4½	–	–	–	–	173	25·05
28–29	–	8	23	1	–	–	–	–	32	25·28
29	–	6½	10	½	–	–	–	–	17	25·15
Totals	7	142	219½	98	83½	97½	78	19½	745	

* For statistical purposes, the middle of the 30th vertebra is regarded as point 29·5, and similarly from each of the other means, 0·5 is subtracted.

In Figure 5, below, the mean positions of D^1 given in the right-hand column of Table I are plotted against the successive positions of the pelvics (curve AB), while the straight line CD is simply the result of plotting the positions of the pelvics both as ordinates and abscissæ. It will be seen that AB and CD cross at point 26·35; that is to say, the first dorsal ray is vertically above the pelvics at this point

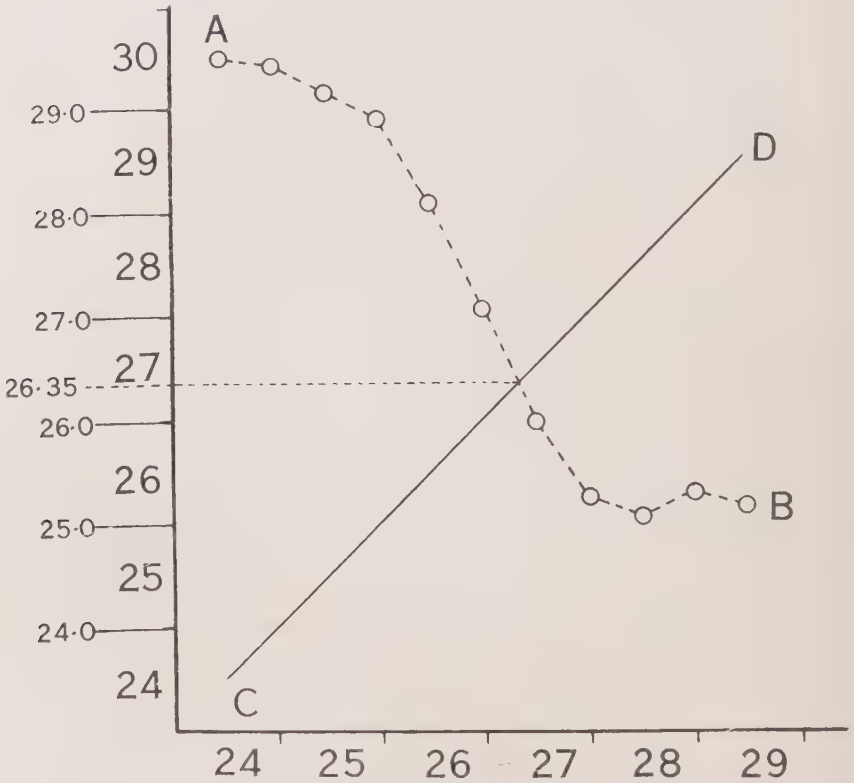


Fig. 5.—The positions of first dorsal ray (ordinates) for observed positions of pelvics (abscissæ) with respect to vertebræ, in fishes with a total of 56 vertebræ, are shown in the graph AB. The successive positions of the pelvics are represented by the straight line CD. The pelvics lie immediately beneath the first dorsal ray at point 26·35 along the vertebral column; i.e. at the level of the anterior part of the 27th vertebra (see text above).

which is approximately the middle of the 27th vertebra. It is also apparent that the dorsal fin and the pelvics continue their movement beyond this stage, so that finally the first dorsal ray comes to lie several vertebræ in front of the pelvics, in contrast with its original position well behind the latter.

Corresponding data for fishes with 56 vertebræ on the position of

the anus with respect to pelvics and vertebræ are given in Table II below :—

TABLE II.

Position of Pelvics. No. of specimens in which pelvics lie beneath vertebræ as under.	Position of Anus. No. of Specimens in which Anus lies beneath vertebræ as under. 41	42	43	44	45	46	Totals.	Position of Anus. Working means.
24	–	–	–	1	½	½	2	44·25*
24–25	–	–	4	6	2½	½	13	43·46
25	–	1	30½	26½	11½	½	70	43·21
25–26	–	1	14½	7½	5	–	28	43·09
26	2½	46½	63	22½	5½	–	140	42·37
26–27	1	18½	19½	4½	½	–	44	42·14
27	4½	87½	73½	4½	–	–	170	41·96
27–28	1	31½	22½	1½	½	–	57	41·96
28	2½	68½	97½	4½	–	–	173	42·10
28–29	–	10	22	–	–	–	32	42·19
29	–	5	11	1	–	–	17	42·26
Totals	11½	269½	358	79½	26	1½	746	

* For statistical purposes, the middle point of the 45th vertebra is regarded as point 44·5, and similarly from each of the other means, 0·5 is subtracted.

The mean positions of the anus are plotted against the successive positions of the pelvics in Figure 6 on page 730. By erecting a perpendicular at point 26·35 along the horizontal axis, and noting the ordinate of the point E at which the perpendicular intersects the curve, we can determine the mean position of the anus when the first dorsal ray is immediately above the pelvics. This occurs when the anus is at point 42·0 or, in other words, when the anus is midway between the 42nd and the 43rd vertebræ. By this time, unlike the dorsal fin, the anus has practically completed its forward movement.

It may not have escaped notice that the curves for both the dorsal fin and anus tend to rise slightly at the right-hand end. This suggests that a slight reversal of the direction of movement relative to vertebræ may take place towards the end of metamorphosis.

Effect of Change in Total Number of Vertebræ.

Data on the position of the first dorsal ray and anus with respect to the pelvics, for fishes with 55 or 57 vertebræ, are given in Tables VII and VIII at the end of this paper. These are summarised graphically in Figure 7, in which the effects of a change in the total number of vertebræ are clearly demonstrated. It is seen that the higher the total number of vertebræ the higher are the mean values for the position of both D^1 and anus for any given position of the pelvics. Thus, the mean position along

the vertebral column at which D^1 is vertically over the pelvics, and the position of the anus at that time, in the three cases is as follows :—

Total No. of vertebræ.	D^1 and Pelvics.	Anus.
55	26·05	41·5
56	26·35	42·0
57	26·60	42·6

Differential Growth as an Explanation of Movements of Fins and Anus.

No proof is here needed of the elementary fact that during the greater part of the relative changes in position of fins and anus, the fish as a whole increases in length. Furthermore, mere inspection first of a larva and then of a newly-metamorphosed fish suffices to verify the fact that

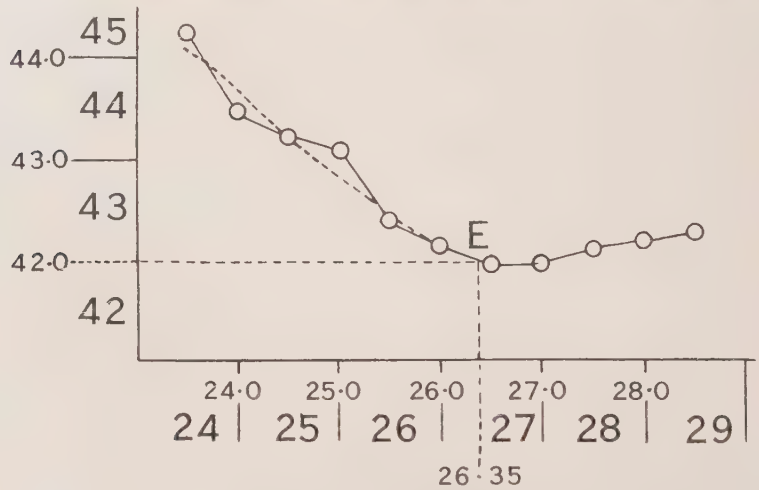


Fig. 6.—The positions of the anus (ordinates) for observed positions of pelvics (abscissæ) with respect to vertebræ, in specimens with a total of 56 vertebræ. The position of the anus when the first dorsal ray is vertically above the pelvics is given by the ordinate of point E, namely, point 42·0 along the vertical column (i.e. beneath the junction of the 42nd and 43rd vertebræ), see text, page 729.

the various body-intervals such as the distance from the pelvics to the anus, or from the anus to the end of the caudal peduncle, form a markedly different proportion of the whole length in the two cases. It would seem a simple additional step to measure selected body-intervals for successive stages in position of fins and anus, and thus to determine in absolute units of length, the growth of each body-interval throughout metamorphosis. The data of the present time-series of samples, however, do not lend themselves to so simple statistical treatment, since the length at which any

given phase of metamorphosis is reached varies over a wide range, and there is much overlap in length among the different phases. The extent and significance of these differences in length form a study of their own and are discussed in a later section of this paper. Despite the fact that

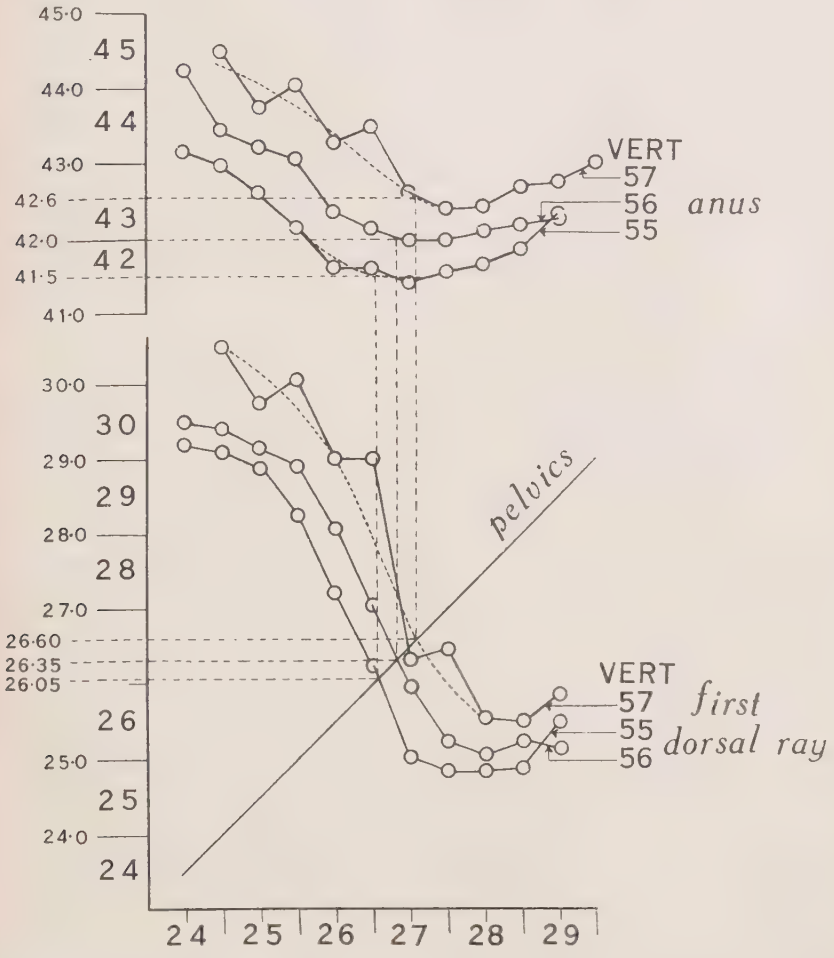
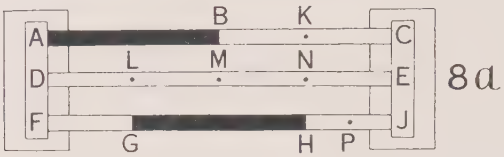


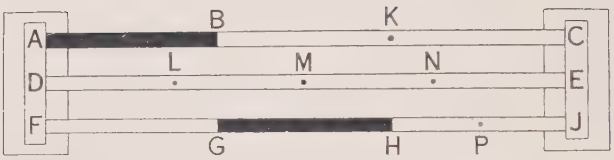
FIG. 7.—Positions of the first dorsal ray and anus (ordinates) for observed positions of the pelvics (abscissæ) with respect to vertebræ in fishes having 55, 56, and 57 vertebræ respectively. The diagram is merely a composite one, combining the results of figures corresponding with those shown in Figs. 5 and 6.

individuals at the same phase of metamorphosis vary in absolute length, it is still possible to watch the change in *proportionate* length shown by given body-intervals from phase to phase. It is found that while some intervals increase in proportion, others decrease. Now a decreasing

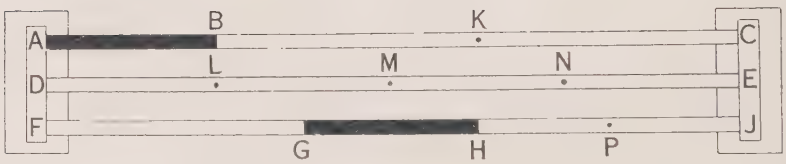
proportion as metamorphosis proceeds may indicate one of three things. In the first place, the body-interval may be actually decreasing in length ; secondly, it may be remaining quite stationary throughout ; or thirdly, it may be increasing in absolute length but at a slower rate than the fish as a whole. A study of the available data has shown that the distance from the pelvics to the anus, and from the back of the brain to the insertion of the first dorsal ray, both undergo a marked reduction in



8a



8b



8c

Fig. 8.—Diagrams illustrating the results of stretching the model composed of tape and elastic described in the text below.

8a.—Unstretched model. Portions AB and GH are constructed of rigid tape : the remaining parts of the three horizontal components are elastic. Total length is 4 units.

8b.—Model stretched to a total length of 6 units.

8c.—Model stretched to a total length of 8 units.

proportion as development proceeds. This observation, as will be realised later, is of great significance as an aid to the understanding of the mechanism of growth during metamorphosis, and in order to demonstrate this point the more clearly, the reader is asked to devote patient attention to the action of some simple models constructed of tape and elastic. The first model is rectangular in form as shown in Figure 8a. It consists essentially of three parallel components AC, DE and FJ, each four units in length, connected at their ends by wooden stays AF and CJ.

The uppermost component AC consists of a tape portion AB of two units in length, and an elastic portion BC, also two units in length. The middle component DE is entirely elastic, being merely marked off into four equal sections at points L, M and N. The third component FJ consists of a portion of tape GH two units long, inserted between single units of elastic FG and HJ. The positions of different points along AC and FJ may be expressed either in units of length from the wooden end AF, or with respect to their position above or below points in any one of the three components. Thus, with the model in its unstretched condition, the following positions may be noted :—

Point.	Distance from AF in units.	Position with reference to points in other components.
B	2	Directly above point M
G	1	,, below ,, L
H	3	,, ,, ,, N

By holding the wooden ends AF and CJ and pulling outwards, the three components may be stretched equally to a new length. As an initial stretching, let the total length be increased from four units to six. Figure 8b represents the new situation. The positions of the three points B, G and H are now seen to be :—

Point.	Distance from AF in units.	Position with reference to points in other components.
B	2	Directly above point G; above but to the left of point M.
G	2	Directly below point B; above but to the right of point L.
H	4	Below but to the left of point N.

A further stretching is now applied so that the total length becomes eight units. Figure 8c reproduces the model at this stage, and the final positions of points B, G and H are :—

Point.	Distance from AF in units.	Position with reference to points in other components.
B	2	Directly above point L; above but to the left of point G.
G	3	Below mid-point between points L and M.
H	5	Below mid-point between points M and N.

Thus, as the result of these two stretchings, the appearance of the model has been greatly changed, and points B, G and H have altered their positions relative to one another and to points along the middle component DE. In addition, the proportions of various parts of the three

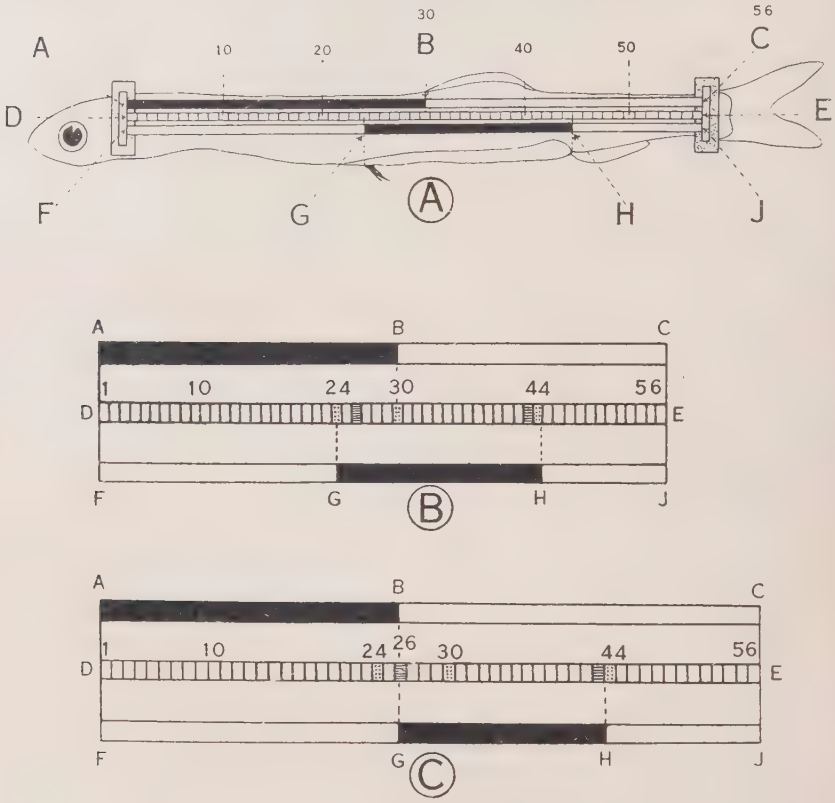


Fig. 9A.—A tape and elastic model, similar in character to that shown in Fig. 8A, is here superimposed on a diagrammatic representation of a post-larval herring, so that points B, G, and H coincide with the pelvics, first dorsal ray and anus respectively with respect to the vertebræ.

Fig. 9B.—Diagram of the model thus created. The middle component is divided into 56 equal parts to represent 56 vertebræ; point B lies above the middle of the 30th vertebra, point G beneath the middle of the 24th vertebra and point H beneath the junction of the 44th and 45th vertebræ.

Fig. 9C.—Diagram representing the model when stretched to a length of 65·1 units as compared with its original length of 56 units. Note how the positions of points B, G and H with respect to vertebræ have changed as the result of stretching.

components have also changed. Dealing first with component AC, it is seen that point B has moved to the left from above point M to above point L, while the distance AB has become reduced in proportion from one-half the total length to one-quarter. Simultaneously, BC has increased in proportion from one-half to three-quarters. The component

DE being entirely elastic extends uniformly throughout its length, so that points L, M and N remain unaltered in relative position along DE. The composite component FJ, on the other hand, has undergone alteration; the elastic portions FG and HJ have each increased from one-fourth of the total length to three-eights, while the rigid tape portion GH has become reduced in proportion from one-half to one-quarter. As the result, point G has moved to the right from its original position beneath point L to a new one between points L and M; and point H to the left from beneath point N to between points N and M.

In Figure 9A a three-component rectangular model is shown superimposed over a diagrammatic outline of a larval herring, so that the different portions of the model roughly represent the body-intervals of the fish over which they fall. In this way we may experiment with a model approximating to the correct proportions of the fish itself. It is seen that this model is only an elaborated counterpart of the simple model just considered, in which point B now represents the position of the first dorsal ray, G coincides with the insertion of the pelvics, and H with the anus. The component DE is here divided into as many blocks as there are vertebræ in the fish—and it may be taken in this instance that there are 56 vertebræ. As before, portions AB and GH in the model can be regarded as rigid and represented by tape, while the remainder is of elastic. For the sake of simplicity, also, all the vertebræ may be considered equal in size (length). Referring back to the data in Tables I and II (pp. 727 and 729) it is noted that with the pelvics situated beneath the middle of the 24th vertebra, the first dorsal ray (represented by point B in the model) lies opposite the middle of the 30th vertebra, and the anus (point H in the model) below the junction of the 44th and 45th vertebræ.

As there are 56 vertebræ in the fish, it will be convenient to regard the total length, AC, of the model as 56 units, so that the dimensions of the model can at once be stated :—

Intervals	AB	BC	FG	GH	HJ
Units of length	29·5	26·5	23·5	20·5	12·0

It is obvious that by stretching the model, points B and H, as in the simple model, will move to the left, relative to points along the centre component DE, and point G to the right. That is to say that the first dorsal ray and the anus will make a forward movement over the vertebræ while the pelvics shift backwards. This is in accordance with fact (p. 727). If stretching is carried sufficiently far, point B (representing the first dorsal ray) can be brought immediately over point G (representing the pelvics). It is possible to calculate the new total length to which the model must be stretched to reproduce this phase, and also the points

along the vertebral column over which the first dorsal ray, the pelvics, and the anus lie :—

Let the new length of the model be x.

Since AB and GH are non-elastic, their lengths remain unaltered throughout the stretching.

With the model in its stretched condition, its dimensions are :

Intervals	AB	BC	FG	GH	HJ
Units of length	29·5	(x—29·5)	$\frac{(x-20\cdot5)\ (23\cdot5)}{(23\cdot5\ +\ 12\cdot0)}$	20·5	$\frac{(x-20\cdot5)\ (12\cdot0)}{(23\cdot5\ +\ 12\cdot0)}$

In this condition AB=FG, or $29\cdot5=\frac{(x-20\cdot5)\ (23\cdot5)}{(23\cdot5+12\cdot0)}$

$$\therefore\ x=65\cdot1$$

Substituting the value 65·1 for x in the above table of dimension :—

Intervals	AB	BC	FG	GH	HJ
Units of length	29·5	35·6	29·5	20·5	15·1

The positions with respect to the vertebræ of points B, G and H are given by :—

Position of B and G $\frac{29\cdot5\times56}{65\cdot1}=25\cdot4$ (i.e. practically opposite the middle of the 26th vertebra.)

Position of H $\frac{(29\cdot5+20\cdot5)\ (56)}{65\cdot1}=43\cdot0$ (i.e. opposite the junction of 43rd and 44th vertebræ.)

Referring back to the data given on page 728 it is seen that the first dorsal ray passes the pelvics at the level of the 27th vertebra, the anus being then at the level of the 43rd vertebra. The model then (see Figs. 9b and c), has brought point B (representing the first dorsal ray) forward at rather too quick a rate, and point H (representing the anus) too slowly, although it has rightly made the total shift greatest in the case of point B (the first dorsal ray).

It was shown on page 730 that the position along the vertebral column at which the first dorsal ray is vertically above the pelvics, and the position of the anus at that time is dependent upon the total number of vertebræ (*vide* Table on p. 730 and Fig. 7 on p. 731). It is easy to see from the model how this could arise, for an alteration in the number of vertebræ means a changing of the number of subdivisions of the middle component DE. With the model stretched to a length of 65·1 units, the intervals along the components AC and FJ will be precisely the same whatever the number of parts into which the centre component DE is divided. Thus, point B will lie immediately above point G at a

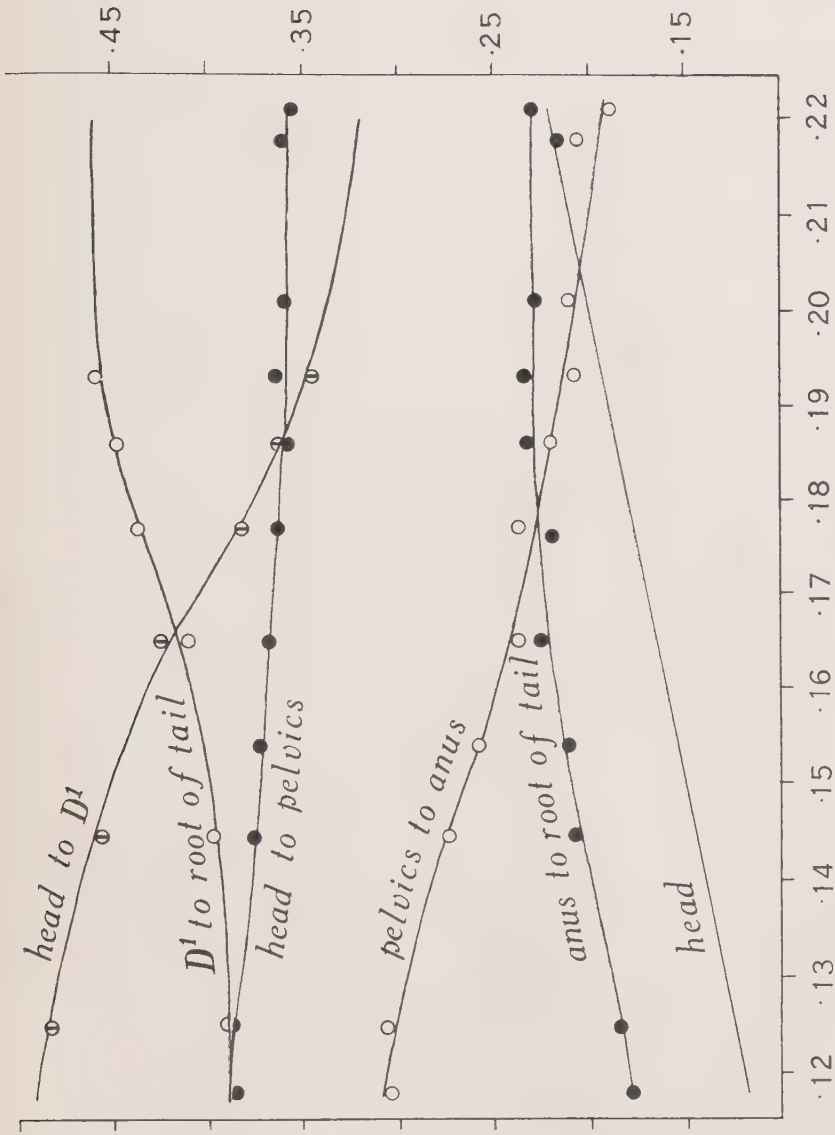


FIG. 10.—Curves showing the proportions of various body-intervals for successive values of the proportion of the head (abscissæ). See Table III on page 739.

distance of 29·5 units from the origin regardless of the division of DE into 55, 56, or 57 parts. But the position along DE to which B and G are opposite will *not* be the same in the three cases :—

1. When DE is divided into 55 parts, points B and G will lie opposite point . . . $\frac{29{\cdot}5\times55}{65{\cdot}1}=24{\cdot}9$ along DE
2. When DE is divided into 56 parts, points B and G will lie opposite point . . . $\frac{29{\cdot}5\times56}{65{\cdot}1}=25{\cdot}4$ along DE
3. When DE is divided into 57 parts, points B and G will lie opposite point . . . $\frac{29{\cdot}5\times57}{65{\cdot}1}=25{\cdot}8$ along DE

Hence the model, like the direct observations on the fish themselves, shows that the higher the number of vertebræ, the higher are the values for the positions of the first dorsal ray, the pelvics and the anus at the same phase of development.

The model is also useful in the study of the change in position relative to vertebræ of the dorsal and anal fins in their entirety. Referring to Figure 8a, the base of the dorsal fin is represented by the anterior portion BK of the component BC. During stretching, point B moves forward with respect to the vertebræ while point C obviously does not. Clearly then, any point between B and C will make some forward movement, the amount depending upon the relative distance of the point from B. Thus point K, representing the hinder end of the base of the dorsal fin, will move forward relative to the vertebræ, but not so quickly as point B. As the result of stretching, the dorsal fin as a whole will appear to move forward and will also tend to cover more and more vertebræ as stretching continues. Similarly with the anal fin. Point H at the anterior end of component HJ moves forward, while point J remains at rest relative to the vertebræ ; point P representing the posterior end of the anal fin will move forward, but at a slower rate than H. Thus the anal fin will tend to move forward and to cover more vertebræ as stretching is applied.

Summarising, it may be said that an elementary model incorporating three distinct systems of differential growth, viz., along the dorsal surface, along the vertebral column and along the ventral surface, respectively, will broadly speaking reproduce the salient features of the relative movements of fins and anus during metamorphosis.

The Changing Proportions of the Body during Metamorphosis.

In the foregoing considerations, attention has been centred mainly on the alteration in relative position of definite points along the dorsal and ventral surfaces of the body and along the vertebral column. It is now necessary to consider the changing proportions of the body-intervals between the moving points. The curves shown in Figure 10 on page 737 are based on data derived from actual measurements of approximately 500 fishes in different phases of metamorphosis, so selected that the whole sequence of transition from the nude post-larva to the scaled and silvery adolescent was represented. The lengths of the different intervals along each fish were determined by direct measurement on a squared rule under magnification, and the absolute measurements then converted into proportions of the body-length L_B of the fish. The resulting data were finally summarised according to the proportionate length of the head, which increases as metamorphosis proceeds, and the mean results were plotted as shown in Figure 10. From these curves the following Table of Values has been prepared :—

TABLE III

Length of Certain Body-intervals Expressed as Proportions of Body-length (L_B).

Head (tip of snout to back of brain).	Head to D^1.	D^1 to end of caudal peduncle.	Head to pelvics.	Pelvics to anus.	Anus to end of caudal peduncle.
·12	·490	·390	·390	·305	·185
·13	·479	·391	·384	·295	·190
·14	·466	·394	·378	·284	·199
·15	·450	·400	·374	·265	·210
·16	·430	·410	·370	·248	·218
·17	·405	·425	·366	·237	·225
·18	·378	·442	·362	·230	·228
·187	**·361**	**·452**	**·361**	**·223**	**·229**
·19	·355	·455	·360	·217	·230
·20	·340	·460	·359	·210	·230
·21	·330	·460	·358	·202	·230
·22	·320	·460	·357	·193	·230

Attention is first directed to the phase of metamorphosis when the first dorsal ray (D^1) lies immediately above the pelvics, i.e. when the distance from the head to the pelvics is equal to that from the head to D^1. It is seen from the above Table that when this occurs the head constitutes ·187 of the body-length. At this stage, also, the length from

the anus to the end of the caudal peduncle has reached a proportionate length slightly exceeding that from the pelvics to anus.

It is of particular interest here to go back to the use of models similar to those employed in previous discussions. The first model, represented in Figure 11a, is similar to that shown in Figure 8a, save that the central component DE need not be used in the present instance, and its dimensions are in accordance with the data in the above Table when the head comprises ·12 of the body-length :—

Intervals.	AB	BC	FG	GH	HJ	Total length of model.
Units of length . .	49	39	39	30·5	18·5	88·0

As before, AB and GH are assumed to be non-elastic and therefore represented by tape, while the remaining intervals are represented by the correct lengths of elastic of uniform grade. The calculated dimensions of this model when it is stretched until AB is equal to FG, as in Figure 11c (representing the phase when the first dorsal ray is vertically over the pelvics) are :—

Intervals.	AB	BC	FG	GH	HJ	Total length of model.
Units of length . .	49	53·8	49	30·5	23·3	102·8

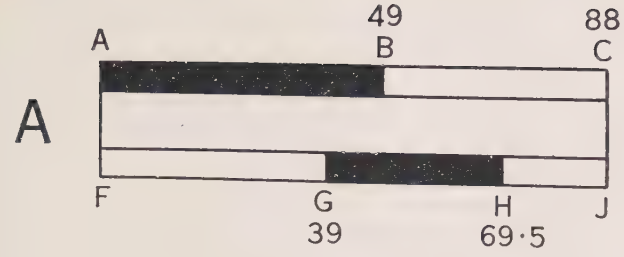
The head of the fish at this phase comprises ·187 of the body-length L_B. The total length of the model (102·8 units) thus represents ·813 L_B, so that $L_B = \frac{102{\cdot}8}{{\cdot}813} = 126{\cdot}4$ units.

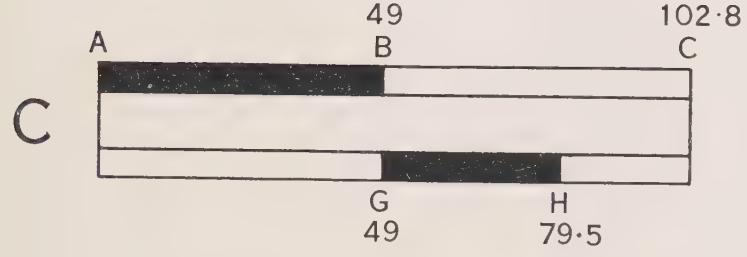
The proportions of the body-intervals as actually determined from measurements of fish, and as represented by the model are, thus, as follows :—

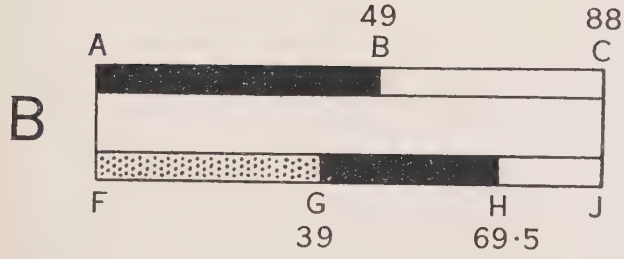
Head.	Head to D^1 (AB)	D^1 to end of caudal peduncle. (BC)	Head to pelvics. (FG)	Pelvics to anus. (GH)	Anus to end of caudal peduncle. (HJ)
Actual ·187 . . .	·361	·452	·361	·223	·229
Model — . . .	·388	·426	·388	·241	·184

It is evident that the model has not reproduced the results from measurements ; AB, FG, and GH are too large, while BC and HJ are too small.

A little experimenting with the model will show that the insertion of a stiffer elastic for the interval FG has an important effect. The model will now have to be stretched to a greater length in order to bring point B over G, and as the result, intervals AB, FG and GH will be







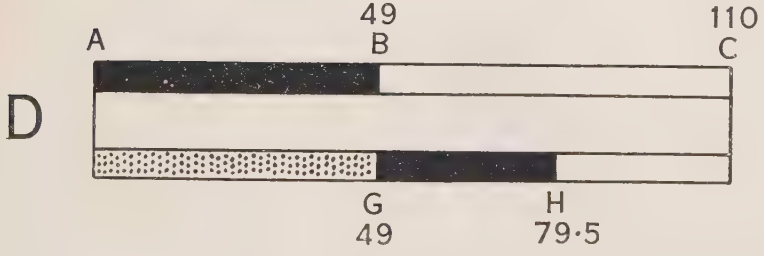


Fig. 11A.—Tape and elastic model described in text on page 740. In this case the interval FG is constructed of elastic similar in stretching quality to the elastic used in the other parts of the model.

Fig. 11B.—A second tape and elastic model, similar in dimensions to that shown in Fig. 11A but differing in that the interval FG is constructed of an elastic $\frac{11}{10}$ times as resistant as the elastic used in other components. This difference is indicated by stippling.

Fig. 11C.—The model shown in Fig. 11A is here stretched until point G lies immediately beneath point B. The total length of the model is 102·8 units.

Fig. 11D.—The model shown in Fig. 11B is here stretched until point G lies immediately beneath point B. The total length of the model is 110 units.

proportionally reduced, while BC and HJ will be increased. Now this is just what is required if the model is to reproduce an exact picture of actual measurements. Imagine then, that BC is constructed of a stiffer elastic of such stretching capacity that it is $\frac{11}{10}$ as resistant to strain as the elastic of which BC and HJ are constructed (Fig. 11b). With this new model stretched until point B is above G (Fig. 11d) the calculated dimensions are :—

AB	BC	FG	GH	HJ	Total length of model.
49	61	49	30·5	30·5	110·0

The new length of the model, 110·0, represents ·813 L_B, and therefore L_B is $\frac{110}{\cdot 813}$=135·3 units.

The proportions of the different intervals of the body as represented by the new model, as compared with actual fish measurements may now be given :—

Head.	Head to D^1. (AB)	D^1 to end of caudal peduncle. (BC)	Head to pelvics. (FG)	Pelvics to anus. (GH)	Anus to end of caudal peduncle. (HJ)
Actual ·187 . . .	·361	·452	·361	·223	·229
New model — . . .	·362	·451	·362	·225	·225

Hence, by the mere substitution of stiffer elastic for the interval BC, the model has been made to reproduce a very satisfactory picture of actual measurements.

By dividing the absolute length of an interval after stretching by its original length, an idea may be obtained of the relative increase made :—

Head.	Head to D^1. (AB)	D^1 to end of caudal peduncle. (BC)	Head to pelvics. (FG)	Pelvics to anus. (GH)	Anus to end of caudal peduncle. (HJ)	L_B
Before stretching						
1·0	1·0	1·0	1·0	1·0	1·0	1·0
After stretching						
2·11	1·0	1·56	1·26	1·0	1·65	1·54

These figures are instructive as showing that with the exception of the two intervals AB and GH which were not allowed to stretch at all, each of the other intervals has enlarged at a rate of its own. The head and the interval HJ have grown at a rate considerably faster than that

of the fish as a whole, whereas BC has grown at approximately the same rate as the fish as a whole, while FG has increased at a much slower rate than these others.

So far, however, growth has only been carried far enough to bring the first dorsal ray above the pelvics, but it has already been shown at an earlier stage that the first dorsal ray travels still farther forward and the pelvics backward, before metamorphosis is complete. Let the model, therefore, be further stretched until its total length is 119·5 units. The lengths of the body-intervals will then be :

AB	BC	FG	GH	HJ	Total length of model.
49	70·5	54·9	30·5	34·1	119·5

Now, for the reason which will presently become clear, the above intervals will be expressed as proportions, not of 119·5 but of $\frac{119{\cdot}5}{1{\cdot}0-0{\cdot}22}$ or 153·5 :—

AB	BC	FG	GH	HJ
·32	·46	·358	·199	·223

Referring back to Table III on page 739, it is seen that when the head comprises ·22 of the body-length L_B, the proportions of the body-intervals vary but little from those given. Thus, by stretching the model to a length of 119·5 units, approximately correct results for a fish whose head comprises ·22 L_B are arrived at. The proportions of GH and HJ are admittedly not entirely accurate, but this is not surprising when it is remembered that by this time the broader features of metamorphosis are practically completed, and the fish is settling down to growth as an adolescent.

It must now be emphasised that the whole of the above considerations have been made possible by arranging that two parts of the model, viz., AB and GH, shall remain at a constant absolute length under all circumstances of stretching. This postulates that in the process of metamorphosis, *the distance from the back of the brain to the first dorsal ray, and the interval between the pelvics and the anus, remain unaltered in absolute length.* Certain it is that if this hypothesis is used in the manner indicated above, reasonably accurate representations of successive phases of metamorphosis can be produced by a simple model. Conceivably these intervals may actually alter slightly in length as the fish grows and differentiates, but the increases cannot be anything approaching those made by other intervals, so that the assumption that there is no change in length is sufficiently accurate for practical purposes.

This conclusion may serve to dispel a possible inclination on the part of the reader to criticise the foregoing paragraphs as a laborious consideration of highly theoretical models composed of tape and elastic, rather than as the presentation of precise data concerning the condition of actual fishes during their transition from larva to adolescent. It is easily realised that if the models lead to a correct understanding of the growth processes during metamorphosis, then it at once becomes possible for workers to foresee the effects of a change of circumstances upon the progress of transition. *Any circumstance which will affect the relative proportions of the initial body-intervals of the larva, or the number of vertebræ, or which at any subsequent stage of metamorphosis will influence the rate of growth of the body-intervals, must inevitably be reflected in the morphological character of the end-result, which in this case is the adolescent fish.* The next section of this paper has to deal with this highly important side of herring investigations, and it will then become apparent how helpful the observations described above can be.

Changes with Time of Sampling.

It has already been pointed out that in a time-series of samples of metamorphosing herrings taken at Plymouth, the length of the fish at which any given phase of transition is reached varies over a wide range, and that there is much overlap in length-range from phase to phase. It is of the greatest practical importance to discover the significance of these differences. Only when this is properly appreciated can we hope correctly to use available biometric data in identifying local forms and races of herrings.

In an endeavour to present an orderly account on this important section of the work, I have found it convenient first to deal with the actual changes in length with time ; next with coincident changes in the average number of vertebræ ; and, finally, to discuss the results in general.

Changes in Length.

As the process of transformation from larva to adolescent herring is one of continuous alteration rather than of abrupt transformation, it is necessary to decide arbitrarily upon convenient criteria of stage of metamorphosis. In the present instance the method is to define the stages according to the positions of the fins and anus with respect to vertebræ. One might equally well adopt as a criterion the degree of development of other characters such as the keeled scales, the general body-scales, or the scheme of pigmentation, or even a combination of such characters. But as data on the relative positions of fins and anus have already been used in the study of the normal process of meta-

morphosis, they may be made to serve here. There is one possible disadvantage in so doing, however, and that is, one must take into account the total number of vertebræ, for, as has already been shown, the relative positions of the fins and anus are dependent upon this factor. This necessitates the statistical treatment of data under separate vertebræ-classes.

On a number of occasions during the months of April and May, 1928, fifty specimens of each of four body-length groups were stained in alizarin, and the position of the fins and anus with respect to vertebræ noted. In Table IV the data on the position of the pelvics in the fishes with a total of 56 vertebræ are summarised :—

TABLE IV

Position of Pelvics with Respect to Vertebræ in Fishes with 56 Vertebræ.

Date 1928	Body-length group (mm.).	Serial No. of vertebra under which pelvics lie.						Total No. of specimens.
		24	25	26	27	28	29	
April 5	30	3·5*	15·5	2·0	–	–	–	21
,, 19	,,	2·5	19·0	10·0	0·5	–	–	32
May 1	,,	1·0	17·0	9·0	–	–	–	27
,, 8	,,	–	10·0	20·5	0·5	–	–	31
,, 18	,,	–	2·5	23·5	7·0	–	–	33
,, 30	,,	–	–	9·5	19·5	2·0	–	31
April 5	35	1·0	14·0	9·5	0·5	–	–	25
,, 19	,,	0·5	1·5	14·5	9·5	–	–	26
May 1	,,	–	6·5	20·0	4·5	–	–	31
,, 8	,,	–	1·5	24·0	10·0	0·5	–	36
,, 18	,,	–	–	11·5	23·5	2·0	–	37
,, 30	,,	–	–	0·5	23·0	10·0	0·5	34
April 19	40	–	–	3·0	8·0	–	–	11
May 1	,,	–	–	8·0	23·5	1·5	–	33
,, 8	,,	–	–	1·5	16·5	10·0	1·0	29
,, 18	,,	–	–	–	15·0	14·5	0·5	34
,, 30	,,	–	–	–	5·5	19·0	2·5	27
May 8	45	–	–	–	3·0	23·5	3·5	30
,, 18	,,	–	–	–	2·0	23·5	1·5	27
,, 30	,,	–	–	–	1·5	21·0	7·5	30

The data of the above table are shown graphically in Figure 12. It will be noticed that in each body-length group, the position of the pelvics tends to fall under a later vertebra in the series as date of sampling gets later. Thus in the 30 mm. body-length group the pelvics on average lie beneath the 25th vertebra on April 5th, but under the 26th and even

* An entry of 0·5 was made when pelvics were below junction of two adjacent vertebræ.

TABLE V. Number of Fish at following Stages of Development.

Date 1928.	Body-length group. (mm.)	Total No. of Fish in sample.	Pelvics in front of First Dorsal Ray (D^1) by :—							Pelvics beneath (D^1)	Pelvics behind First Dorsal Ray (D^1) by :—			
			$6\frac{1}{2}$ vert.	6 or $5\frac{1}{2}$ vert.	5 or $4\frac{1}{2}$ vert.	4 or $3\frac{1}{2}$ vert.	3 or $2\frac{1}{2}$ vert.	2 or $1\frac{1}{2}$ vert.	1 or $\frac{1}{2}$ vert.	0	$\frac{1}{2}$ or 1 vert.	$1\frac{1}{2}$ or 2 vert.	$2\frac{1}{2}$ or 3 vert.	$3\frac{1}{2}$ or 4 vert.
April 5		50	6	28	16	–	–	–	–	–	–	–	–	–
April 19		51	–	8	20	15	7	1	–	–	–	–	–	–
May 1	30	52	–	7	14	22	6	1	2	–	–	–	–	–
May 8		50	–	4	14	20	12	–	–	–	–	–	–	–
May 18		46	–	–	3	2	15	21	4	1	–	–	–	–
May 30		50	–	–	1	1	–	7	7	16	13	5	1	–
April 5		50	–	3	18	26	3	–	–	–	–	–	–	–
April 19		51	–	1	2	10	13	10	10	4	1	–	–	–
May 1	35	51	–	–	1	13	17	12	4	4	–	–	–	–
May 8		49	–	–	–	7	19	15	2	4	2	–	–	–
May 18		50	–	–	–	–	–	5	19	13	12	1	–	–
May 30		51	–	–	–	–	–	–	–	5	16	19	11	–
April 19		15	–	–	–	–	–	1	3	7	4	–	–	–
May 1		51	–	–	–	–	–	4	6	18	16	7	–	–
May 8	40	50	–	–	–	–	–	–	1	9	17	21	2	–
May 18		51	–	–	–	–	–	–	–	–	9	28	14	–
May 30		54	–	–	–	–	–	–	–	–	–	19	29	6
May 8		51	–	–	–	–	–	–	–	–	1	25	25	–
May 18	45	50	–	–	–	–	–	–	–	–	–	21	28	1
May 30		52	–	–	–	–	–	–	–	–	–	12	35	5

the 27th towards the end of May. It is also seen that the fishes of the 30 mm. body-length group taken on May 30th are, so far as the position of the pelvics is concerned, practically as far advanced as those of the 40-mm. group on April 19th.

This change in position of the pelvics with time is accompanied by corresponding changes in position of the dorsal fin and anus, as well as by changes in pigmentation and degree of development of the scales. Furthermore, similar results are obtained when the data for fishes having a total of 55 or 57 vertebræ are used instead of those of fishes with 56 vertebræ. Clearly, then, it may be said that the later the sample is taken the more advanced in metamorphosis are the individuals of any given body-length group, and in order further to impress this fact, Table V has been prepared showing the number of fishes in each of a series of classes according to the position of the first dorsal ray (D^1) relative to the pelvics.

Using the 30 mm. body-length group as an example, it is seen that the specimens taken on April 5th are all relatively early transition stages in which the pelvics are at least $4\frac{1}{2}$ vertebræ in front of the first dorsal ray (D^1), whereas those of May

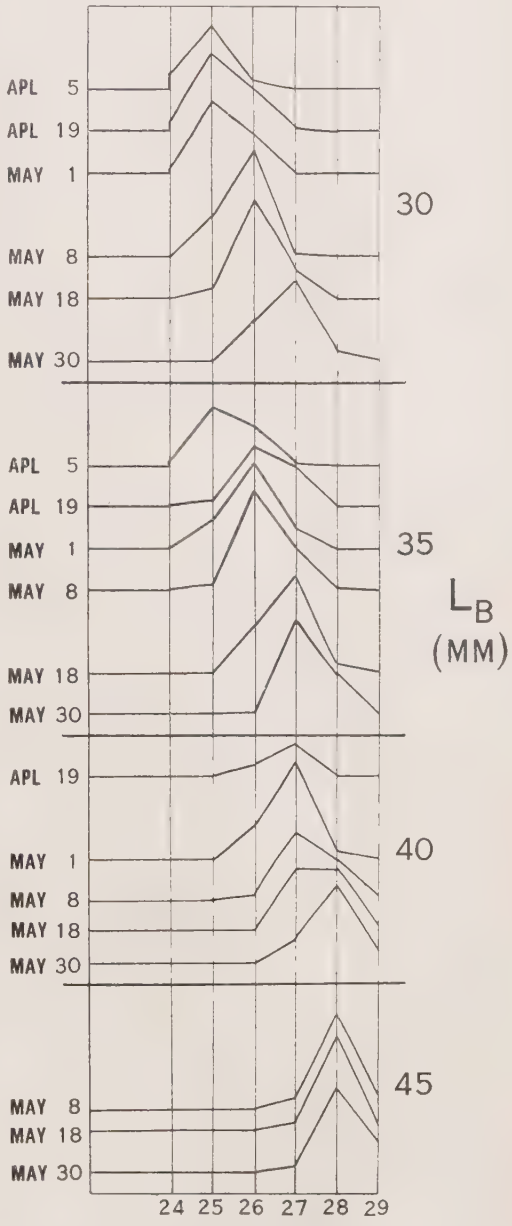


Fig. 12.—Graphic representation of data given in Table IV on page 745.

30th are much more advanced stages in which the pelvics are on average immediately beneath D^1.

Stating the matter in another way, it may be said that for any stage of metamorphosis the length in later samples is shorter than that in earlier ones. This may be illustrated by extracting the data from Table V relative to the stage when the pelvics lie beneath the first dorsal ray :—

Date 1928.	Body-length Groups (mm.). 30	35	40
April 19	–	4	7
May 1	–	4	18
,, 8	–	4	9
,, 18	1	13	–
,, 30	16	5	–

Thus, on April 19th and May 1st, this stage of development was not reached until a length of 40 mm. had been attained ; on May 18th specimens of 35 mm. were at this stage, and on May 30th, those of the 30 mm. group. Similar data could, if necessary, be produced to show that during the months of May and June of the year 1929, this phenomenon was again apparent, so that it may be regarded as a frequent and probably normal occurrence.

Change in the Average Number of Vertebræ.

It has been shown above that the individuals of a given length-group are more advanced in metamorphosis in later samples than in earlier ones. It is instructive next to consider the value of the average number of vertebræ in the same fishes. In Table VI relevant data are shown for individuals of the 30-mm. and 35-mm. groups :—

TABLE VI.

Body-length group (mm.).	No. of Vertebræ	Date of Sample (1928) April 5	April 19	May 1	May 8	May 18	May 30
30	54	–	1	1	–	–	–
	55	26	15	17	13	7	14
	56	21	32	27	31	33	30
	57	3	3	5	6	5	2
	Average	*55·54*	*55·73*	*55·72*	*55·86*	*55·95*	*55·74*
35	54	2	1	–	–	–	–
	55	15	17	16	9	7	14
	56	25	26	31	36	37	34
	57	7	4	3	3	6	1
	58	–	1	–	–	–	–
	Average	*55·73*	*55·735*	*55·74*	*55·86*	*55·98*	*55·735*

The data show that the average number of vertebræ does not remain constant throughout the series of samples; on the contrary, there is a definite tendency for it to rise as the sampling is later.

A number of instances might be given which would show that within the same day's sampling, the average number of vertebræ changes with the body-length group. The following two cases are worthy of mention because they demonstrate to a marked degree how the average may change :—

Date of Sample.	No. of Vertebræ	Body-length Group (mm.). 30	35	40	45	50	55	60	65
	55	1	2	10	17	–	–	–	–
May 26th,	56	28	30	31	28	–	–	–	
1927	57	21	17	8	5	–	–	–	–
	58	1	1	1	–	–	–	–	–
	Average	*56·44*	*56·34*	*56·00*	*55·76*				
	54	–	–	–	–	–	–	1	1
June 25th,	55	–	–	–	–	7	9	18	16
1928	56	–	–	–	–	40	35	27	28
	57	–	–	–	–	3	6	4	5
	Average					*55·92*	*55·94*	*55·68*	*55·74*

One particular point of interest is plainly demonstrated by the data for May 26th, 1927. It will be noticed that the average number of vertebræ for the individuals of the 30-mm. group is the highest and that for the 45-mm. group the lowest. It should also be noted that the fishes of the 30-mm. group are the least advanced in development, and those of the 45-mm. group almost completely metamorphosed. Thus, *within the same sample,* a lower average number of vertebræ coincides with a more advanced stage of metamorphosis.

Significance of Results in "Racial Investigations."

It is hardly necessary to point out that the observations described above raise questions of great significance to herring biologists engaged in what have come to be known as "racial investigations." Why should the length at any given phase of metamorphosis tend to decrease as the time of sampling gets later? Why, simultaneously, should the average number of vertebræ tend to rise? To what extent are these facts due to differences between the adult fishes which produced the larvæ, and how much is due to the variation in physical conditions under which the eggs were incubated and the larvæ developed? On his answers to these questions will depend an investigator's interpretation of those significant differences which he frequently observes between random samples of herrings. In the opinion of the present writer we cannot confidently assess the significance of these differences until we know from actual

experiment the extent to which the biometric characters of a new generation may differ from those of their parents as the result of the physical conditions under which development takes place. Thus, in the present instance, who can say whether the diminishing length of a given phase of metamorphosis and the simultaneous increase in average number of vertebræ was due more to the fact that the larvæ had sprung from different parent-stocks, than, say, to the effects of contemporary changes of temperature over the area during the season of incubation and development of the larvæ ? Past work has certainly shown that the spawning shoals visiting Plymouth waters are by no means uniform in morphological character ; but it is equally true that the temperature undergoes marked change, falling first to a minimum and then gradually rising again. Larvæ incubated and developed at a relatively low temperature might be expected to require a longer time than those reared at a higher temperature to reach a certain stage ; the size at which this stage is reached would probably be larger.*

In addition, there is some reason for supposing that at the lower temperature, the number of vertebræ would tend to be higher. Such expectations, if applied to the particular local circumstances, will produce results which fit the observed facts quite as reasonably as the hypothesis of purely hereditary influences. But in the absence of relevant knowledge, it is impossible to say how much either has played in producing the end-result. In general, therefore, although quite real biometric differences are observable between random samples of herrings, their interpretation is still open to question and will remain so until experimental work has yielded that fundamental knowledge which alone can render interpretation possible.

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* Gray (**4**, p. 129), for example, has shown experimentally that when trout eggs are incubated at low temperatures the embryos at the moment of hatching are significantly larger than those hatching from eggs which have been incubated at higher temperatures. Increasing the temperature of incubation increases the growth-rate of the embryo, but, at the end of larval life, the full-time embryo is smaller than after slower development at a lower temperature. At higher temperatures, a larger proportion of the available yolk is required for the maintenance of the embryo, leaving a smaller proportion available for the formation of new tissue.

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TABLE VII.

Position of Pelvics. No. of specimens in which pelvics lie beneath vertebræ as under.	Total No. of vertebræ.	Position of 1st Dorsal Ray (D^1). No. of Specimens in which D^1 lies above vertebræ as under. 24	25	26	27	28	29	30	31	Totals.	Position of D^1. Working means.*
24		–	–	–	–	1	3	9	1	14	29·21*
24–25		–	–	–	–	–	4½	9	1½	15	29·10
25		–	–	–	–	7	20	17	4	48	28·87
25–26		–	–	–	1	4½	8	2½	–	16	28·25
26		–	1½	6	13	17	12½	1	–	51	27·21
26–27	55	–	1½	7½	5½	3½	1	–	–	19	26·24
27		1	33½	16	7½	–	–	–	–	58	25·02
27–28		1½	12	8	½	–	–	–	–	22	24·84
28		3½	37	24½	–	–	–	–	–	65	24·82
28–29		–	5	3	–	–	–	–	–	8	24·87
29		–	–	3	–	–	–	–	–	3	25·5
Totals		6	90½	68	27½	33	49	38½	6½	319	
24–25		–	–	–	–	–	–	–	1	1	30·5
25		–	–	–	–	–	3	4	4	11	29·75
25–26		–	–	–	–	–	–	3½	4½	8	30·06
26		–	–	–	–	2½	5	8	1½	17	29·0
26–27		–	–	–	–	½	½	2	–	3	29·0
27	57	½	1½	11½	14½	3	2	1	–	34	26·32
27–28		–	½	4½	5	3	1	–	–	14	26·46
28		–	9½	23	9½	½	½	–	–	43	25·56
28–29		–	–	6	–	–	–	–	–	6	25·5
29		–	½	3	2½	–	–	–	–	6	25·83
29–30		–	1	–	–	–	–	–	–	1	24·5
Totals		½	13	48	31½	9½	12	18½	11	144	

* For statistical purposes, the middle point of the 30th vertebra is regarded as point 29·5.

TABLE VIII.

Position of Pelvics. No. of specimens in which pelvics lie beneath vertebræ as under.	Total No. of vertebræ.	Position of Anus. No. of Specimens in which Anus lies beneath vertebræ as under. 41	42	43	44	45	46	Totals.	Position of Anus. Working means.*
24		–	1	2½	8½	1	–	13	43·23*
24·25		–	1	6	6	1	–	14	43·0
25		–	11	21½	12	2½	–	47	42·63
25–26		–	7½	6½	2	–	–	16	42·16
26		8	30	11	2	–	–	51	41·64
26–27	55	4½	8½	5½	½	–	–	19	41·61
27		10½	44	5½	–	–		60	41·42
27–28		2½	15½	4	–	–	–	22	41·57
28		3½	46½	14	–	–	–	64	41·66
28–29		–	5	3	–	–	–	8	41·87
29		–	½	2½	–	–	–	3	42·33
Totals		29	170½	82	31	4½		317	
24–25		–	–	–	–	1	–	1	44·5
25		–	–	½	7	2	½	10	43·75
25–26		–	–	–	5	4½	½	10	44·05
26		–	½	4	11	1½	–	17	43·29
26–27	57	–	–	1	1	1	–	3	43·5
27		–	4½	22½	5½	1½	–	34	42·62
27–28		–	4	9½	2½	–	–	16	42·41
28		–	6½	32½	4	–	–	43	42·44
28–29		–	–	5	1	–	–	6	42·67
29		–	–	4½	1½	–	–	6	42·75
29–30		–	–	½	½	–	–	1	43·0
Totals		–	15½	80	39	11½	1	147	

* For statistical purposes, the middle point of the 44th vertebra is regarded as point 43·5.

On the Occurrence and Habits of the Siphonophore, *Stephanomia bijuga* (Delle Chiaje).

By

N. J. Berrill,

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With One Figure in the Text.

According to E. T. Browne, 1899, *Stephanomia bijuga* (Delle Chiaje) (syn. *Cupulita sarsii* Haeckel and *Agalmopsis elegans* Sars, partim) belongs to the surface Atlantic fauna. It has been recorded at Valencia from March to November, and while suffering badly from the destructive power of gales it must occur at times in enormous numbers, for in November, 1898, tow-nets were taken that were full of isolated pneumatophores. Into the more confined waters of the English Channel, however, it penetrates apparently very rarely, the only record being that of a single specimen taken a mile or two out from Plymouth Sound in March, 1902.

It is of some interest, therefore, to record its occurrence in great numbers in the main and secondary channels of the Salcombe Estuary, even to the heads of the tidal creeks, on May 17–19, 1929. This profusion coincided with a similar abundance of the three Ctenophores commonly occurring in these waters, namely, *Beroe cucumis* Fabricius, *Bolina infundibulum* Fabricius, and *Pleurobrachia pileus* Fabricius, and not only were these abundant, but they also had reached what is possibly their maximum size. Individuals of Beroe frequently were seen of at least six inches in length. Ten days later all trace of Siphonophores and Ctenophores had vanished, with the exception of some small individuals of Beroe, and these last were not seen to approach the large size already mentioned until after two months.

Stephanomia was noticed floating and swimming a few inches below the surface of very calm water, though all that was visible was the red pigment of the gastrozoids, but as several individuals were obtained in perfect condition and were kept alive in glass vessels for some days, a description of its form and behaviour may be of some interest. Unfortunately no microscope or lens was available, so that only the coarser details were observed.

The general form is seen in Figure 1 A, which is typical of the great

majority of the individuals encountered, i.e. two to three inches in length and with three or four sets of nectophores ; but apart from the details shown in the figure, the observations more concerned the habits than the anatomy.

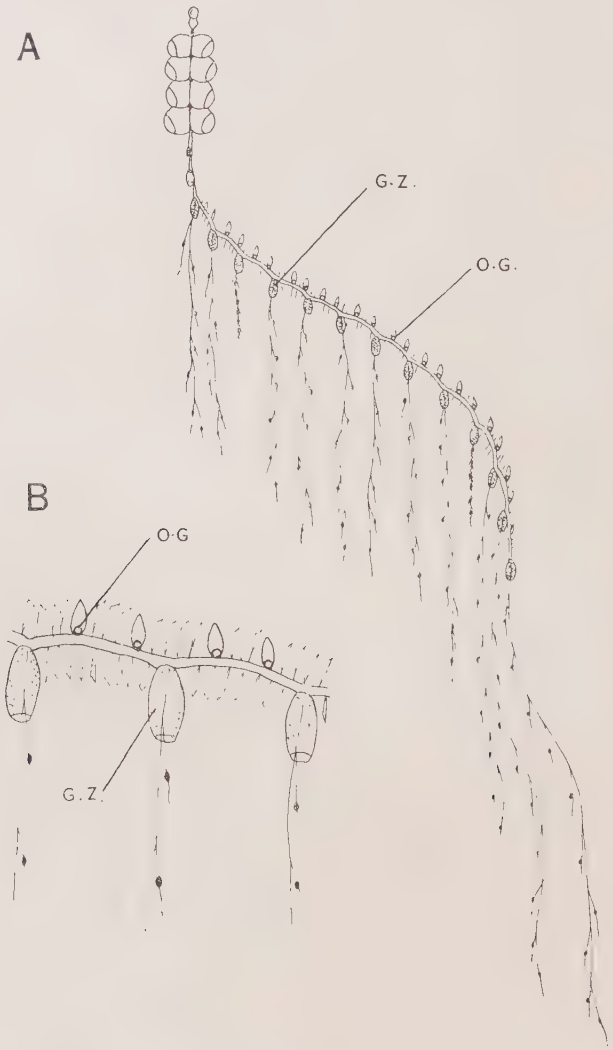

Fig. 1.

Unless disturbed, Stephanomia apparently remains perfectly quiescent, and in an inclined position. The pneumatophore causes the whole organism to float to the top of still water, and that part of the stem bearing the nectophores hangs vertically below it, but the rest of the

stem falls away from the basal nectophores at an angle of about forty-five degrees. The reason for this seems obvious, for in this position the long contractile filaments hang separately, vertically, and evenly spaced, whereas if the whole organism assumed a vertical position in the quiescent state the filaments would hang down together as one cluster, with a relatively small volume of water with its contained organisms exposed to their influence.

The result, therefore, of the inclined position is to form, in effect, a very efficient trap for small actively moving organisms such as copepods. Undisturbed, the Stephanomia drifts placidly with the current and consequently small active forms are in constant danger of swimming into the grating of filaments as herring are into a drift-net. Contact of any small particle with a single filament or tentacle causes the instantaneous contraction of the latter towards its associated gastrozoid. Stronger stimulation of one or more filaments not only results in their contraction, but also that of the stem itself up to the base of the nectophores. Usually such stimulation also affects the nectophores so that the organism moves actively away. Sometimes, however, the swimming movements seem to start spontaneously, and an individual suddenly swims through the water at about 8 cm. per second, setting into motion also any with which it may collide. At 16° C., to produce the above movement, the nectophores contract simultaneously about four times per second.

The characteristic inclined position when quiescent is apparently due to the presence of an oil-globule in two persons, that may be modified bracts, occurring between every pair of gastrozoids, as is shown in Figure 1 B. Typical bracts are numerous on all sides of the stem between the gastrozoids, but the forms containing an oil-globule are to be found only on its upper side, opposite to that bearing the gastrozoids themselves.

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An Apparatus for Keeping Marine Organisms Under Circulation in Narrow Observational Tanks.

By
A. J. Grove, M.A., D.Sc.

With 1 Figure in the Text.

This apparatus was elaborated during some preliminary observations on the biology of the polychæte worm *Melinna adriatica*, and in view of its possibilities for facilitating observations on other small marine organisms, an account of it seems desirable.

Tanks sufficiently narrow to enable the worms in their long slender tubes to remain in position near to the sides in order that the organism might be observed with a hand lens or binocular microscope, were made from two sheets of glass separated by a piece of rubber tubing bent into an arc, and the whole clipped tightly together by means of six spring washing pegs. By the use of tubing of different thicknesses, tanks of different widths can be made according to the material used and type of observation desired. A simple support for the tank was made from a block of wood in which were bored two holes to hold the lower clips. In practice, such tanks were found to be practically water-tight, but to protect the bench it was found convenient to place the block in a shallow tray.

Such tanks enabled the worms to be kept under close observation, but owing to their narrowness the quantity of water contained in them was small, and for extended observational work it was desirable that a circulation of freshly aerated water should be established. This was effected by a modification of the circulating system for aquaria previously described (Cannon and Grove, 1927), and the arrangement is seen in Figure 1.

The tank A is connected by siphons to a jar B on one side, and a shallow vessel C on the other. The ends of the siphons dipping into the tank have to be drawn out because of the narrowness of the tank. One should dip lower into the tank than the other. Jar B* is connected by a wide siphon with the circulating jar in which is suspended the air-blast tube, the drawn-out, turned-up end of which enters the circulating tube which passes

* Jar B is not absolutely essential. The siphon from the tank could pass directly into the circulating jar, but the insertion of the jar between the tank and the circulating jar was found convenient during manipulation, and, as mentioned later, if other tanks are inserted in the circulation.

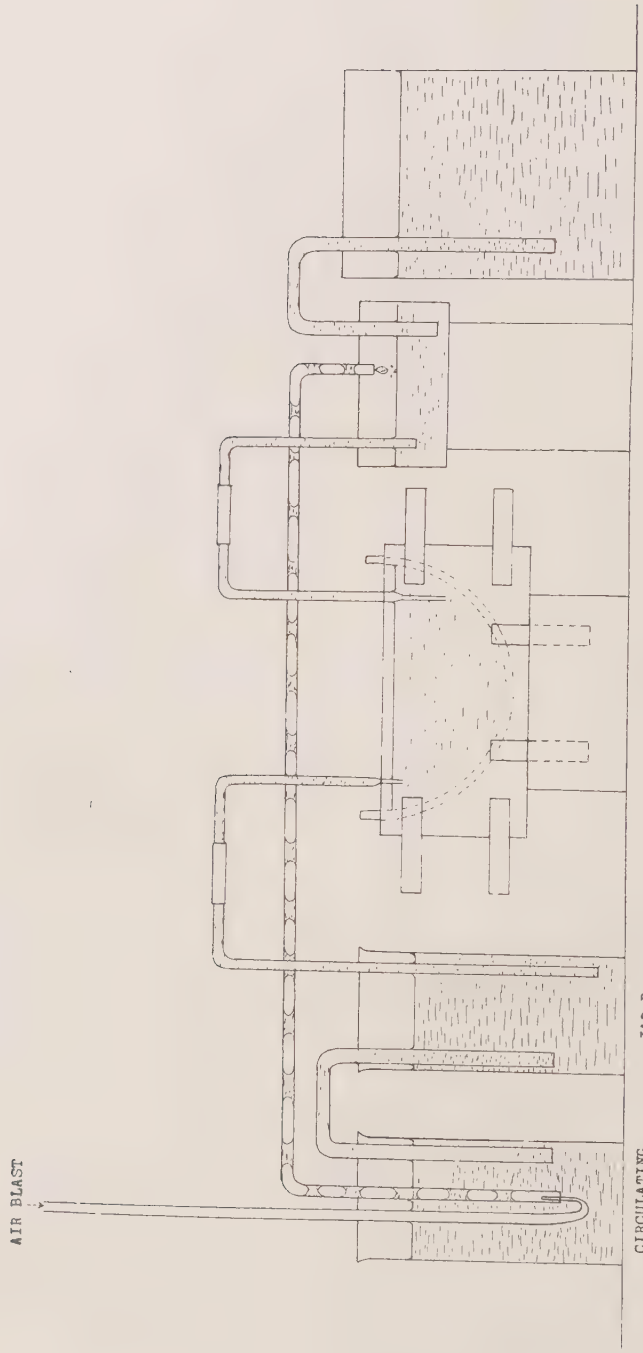

FIG. 1.

thence to vessel C. When the air blast is turned on, a stream of bubbles of air and water pass along from the circulating jar to the vessel C. This tends to lower the level of the water in the circulating jar, to compensate for which water is drawn from jar B through the tank A from vessel C, establishing a circulation. Because, however, of the fineness of the drawn-out ends of the siphons dipping into the tank, the flow of water through the tank to the circulating jar is slower than that from the circulating jar to vessel C by way of the circulating tube. There is therefore a tendency for vessel C to overflow and a big difference of level of water to be established between vessel C and the circulating jar. This difficulty was overcome by connecting vessel C by means of a siphon with a wide jar D. Then, a considerable quantity of water would have to be carried over by the circulating tube before the level in C and D would be raised sufficiently for flooding to occur.

With the apparatus arranged in this way, after the circulation has been running for a short time, an equilibrium is set up so that a difference of level (depending on the rate of flow in the circulating tube and the size of the narrow ends of the tank siphons) is maintained between the vessel C and jar B, giving an indication of the rate of flow of water through the tank.

The following points were found to require attention in order that the apparatus may work efficiently. The drawn-out ends of the tank siphons should be made carefully to fit into the tank, and it is essential that the inflow siphon should be wider than the outflow, otherwise the tank is apt to be emptied to the level of the outflow siphon because water cannot enter from the inflow sufficiently rapidly. In the apparatus used, the inflow siphon was the lower one, because a flow of water along the surface of the mud in the tank without it being stirred up was desired. The reverse arrangement would work equally well. It will be found convenient for manipulation if the tank siphons are made in two pieces joined together by rubber tubing. This is a convenience when placing them in position, for after filling, a siphon can be maintained full of water by pinching the rubber tubing and the two ends are free to be inserted into the tank or jar as the case may be.

The vessel C should be of convenient size (a finger bowl was actually used) so that there is as much surface as possible while the shallowness will ensure that only freshly aerated water passes into the tank. If a deeper jar is used there is some danger of stagnation in the lower part of the jar.

In the first trials the tank was made of ordinary glass, but from various observations it was found that the worms were in all probability negatively phototropic and the simplicity of construction of the tanks enabled a number of tentative experiments to be carried out on the use of coloured

lights, for, by using glass of different colours for the sides of the tank, the activities of the animals under these varying conditions could be tested until the most suitable was found.

The figure gives the arrangement for one tank, but if it is so desired (as in parallel phototropic experiments with different coloured glasses), other tanks can be inserted into the circulation. It is essential, of course, that for each tank the inflow siphon should come direct from vessel C, the outflow passing into a convenient jar which is in siphonal connection with B.

The air blast for the circulation was taken in the original experiments from the Laboratory system, but where such is not available, the simply made pump described previously (Cannon and Grove, 1927) can be substituted.

If the observations are to extend over a lengthy period, it may be necessary to change the water in the safety jar D occasionally, for it is obvious that when the apparatus is running continuously and the equilibrium has become established, the water in this jar does not enter into the circulation, and is consequently likely to become foul.

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Preliminary Notes on the Bionomics of the Amphipod, *Corophium volutator* Pallas.

By

T. J. Hart, B.Sc.

With 4 Figures in the Text.

Introduction and Previous Work.

The Amphipod *Corophium volutator* Pallas has been described, mainly from a purely systematic standpoint, under the synonyms *C. grossipes* Linnæus, *C. longicorne* Latreille, and *C. bicaudatum* Linneo (Della Valle). Stebbing in his standard work (**19**) on the Gammaridea, accepts *volutator* as the earliest, and modern French and Danish authors follow him.

Corophium volutator is found in the greatest abundance on certain mudflats in estuarine areas round the coasts of N.W. Europe, but by no means everywhere. It appears that the nature of the substratum and the salinity of the water are two of the main factors leading to its localized distribution, and accordingly an investigation of the conditions which define its habitat is likely to throw light on some very interesting problems. These notes record the first stages of such an investigation, together with a study of the intimately related problems of the feeding habits and life-cycle of the animal.

It seems that no detailed account of the feeding mechanism of any Amphipod has yet been published; though Hunt (**11**) gives a short and pithy description of a "filter-feeding" mechanism in Ampelisca. This author classes most of the Amphipoda he deals with as selective deposit feeders, but states that though this is true in so far as they are bottom-living forms, the actual mechanism is probably more often of a type such as would lead to their being classed under his scheme as suspension-feeders. However, it seems obvious from a study of their appendages that some Amphipoda do not possess a filtering mechanism, while it is highly probable that many more combine the habit of feeding on larger particles with filter feeding, as Cannon has found in several of the lower Malacostraca.

Corophium volutator approaches this last type, though, as would be expected from its peculiar habitat, the feeding methods are somewhat specialised and probably differ in detail from those of Amphipoda generally.

As regards the life-cycle, Blegvad (**3**) in his exhaustive study of *Gammarus locusta* from this standpoint has summarised the scanty observations of previous workers. He gives good reasons for supposing that a life-cycle of a certain type is common to a number of littoral Amphipoda of widely different genera. Several broods are hatched each year, the last brood maturing slowly through the winter and commencing to breed in the following spring. Most of the adult individuals of the previous year die off during the winter, but a few breed again in the late winter and early spring. These species are thus annual or nearly so.

While my material has so far been insufficient for the results to be conclusive, they seem to show a life-cycle of an essentially similar type for *Corophium volutator*.

Sexton's wonderful work on the moulting and growth stages of Gammarus (**16**) furnishes the only exact information on these points in the whole of Amphipod literature. Her method is to isolate the just hatched young and collect all the moults from that stage onwards *from one individual*. Thus this method applies only to animals reared under aquarium conditions. *Corophium volutator* does not, like *Gammarus chevreuxi* Sexton, breed all the year round (not, at any rate, in the North), and, as most of my work was done perforce during the winter, I could not, most unfortunately, follow it up on these lines. Enough has been gathered from detailed observations of material obtained at different times of the year, to anticipate most interesting and important results from an investigation of Corophium by this method.

The bulk of this work having been presented as a degree thesis at the University of Leeds, I have to thank Prof. Garstang for permission to publish, also for suggesting the work in the first instance, and for help and encouragement throughout. Through the kindness of Dr. Allen, I was able to carry on the work at the Marine Biological Laboratory at Plymouth for three weeks during April, 1929, and so was able to study Corophium from a widely different locality. I have to thank several members of the staff, in particular Mrs. Sexton, Dr. Orton, and Mr. Ford, for much valuable advice and encouragement, and would like in conclusion to pay tribute to the entire working staff for the great kindness with which I was received.

Material and Methods.

The bulk of the material on which these observations are based was obtained from Whitby harbour. In April, when working at the Plymouth Laboratory, a few Corophium were obtained from the mud-flat between Ditchend and Southpool lake in the Salcombe estuary, and a fairly abundant material from the Cornish bank of the River Tamar, $\frac{1}{2}$ mile below Calstock, where the dilution is considerable.

In August, 1929, a rich material of Corophium was found in some of the tidal creeks around Blakeney Point, Norfolk, one batch in distinctly brackish water. Unfortunately I have not yet been able to work up this material in detail, but some information gained has been incorporated in this note.

At Whitby, on the W. side of the low-water channel above the bridge, opposite the L. & N.E.R. goods yard, there is a wide expanse of moderately soft, uniform, grey mud, traversed by but few small runnels, and uncovered at about half-tide. In this mud *Corophium volutator* forms the dominant species of the animal community. In bright sunny weather Corophium could be found crawling freely over the surface, and could easily be collected in large numbers. It soon became apparent that only the larger individuals were being captured in this way, and accordingly an attempt was made to devise a simple method of collecting fairly large numbers which, if not giving a really true index of the density of population, at any rate seemed to ensure a fair proportion of the smaller individuals being caught. The procedure was as follows :—

The mud over an area of 1 sq. metre was scooped up to a depth of about 5 in. (about the maximum depth of Corophium burrows) and passed through a wire sieve of 1 sq. mm. mesh. The Corophium left amongst the larger detritus were then picked out with forceps. Even so it was found that comparatively few of the smaller free-living young were caught, but it was impossible to use a smaller mesh, as the work was thereby rendered so slow that even 1 sq. m. of mud could not be worked in one intertidal period. Accordingly 500 c.c. samples of mud were taken and sieved out at leisure in the laboratory, thus affording a rough indication of the numbers of young present.

In attempting further to elucidate the nature of the life-cycle, living Corophium, caught in October, were successfully kept in an aerated tank, supplied with mud, sea-water, and a circulating apparatus in the laboratory at Leeds for a considerable period, but the animal does not seem to breed in winter, not, at any rate, in the North, and unfortunately during the great frost of February, 1929, the heating was kept on day and night and the animals incontinently perished.

I was therefore forced to rely largely upon measurement investigations of the type evolved by Blegvad (**3**) in his great work on the Biology of *Gammarus locusta*. As I was only able to make four quantitative collections from Whitby : in July, October, and December, 1928, and March, 1929, these measurements can hardly be considered really critical. A further sample, very kindly sent to me by Mr. George Duke of Robin Hood's Bay on April 13th, helped to strengthen the argument considerably, and in conjunction with a careful examination of each specimen as it was measured, a life-cycle of a type essentially similar to that postulated

by Blegvad (*loc. cit.*) for a number of littoral Amphipoda, seemed to be disclosed. I therefore considered it worth while tabulating the results, in the hope of vindicating them by a more thorough investigation in the future.

The method of measuring employed was the same as that described by Blegvad: the animals were extended on a millimetre scale under a dissecting microscope and the length taken from telson to rostrum.

To gain an accurate idea of the nature of the substratum in which *Corophium volutator* lives, samples of mud from the different localities worked were graded and analysed for organic content by the method used by Allen (**1**) for classifying bottom-deposits.

The salinity range of the water in the natural habitat of this species must be considerable, and constantly varying. Some estimations by silver nitrate titration were made, however, with a view to comparing the probable range in the different localities. To determine the change in salinity which the animals could actually endure, small numbers were isolated under different conditions, with a small amount of mud from their natural habitat.

To ascertain the nature of the food, small numbers of living Corophium were kept under various conditions in finger bowls and small dishes, aerated with a pipette at definite intervals. Strips of Ulva, Enteromorpha, and decaying deciduous leaves were tried as food, but without success, as it appears that the animals feed on smaller particles of organic detritus. When mud from the natural habitat was supplied, small winter-caught Corophium could be kept almost indefinitely under these conditions.

The actual feeding process was observed partly by fixing the animal on its back in a capsule of sea-water with plasticine, and using a dissecting microscope, and partly by enclosing living individuals against the side of a rectangular slide-trough and observing them with binocular mounted horizontally.

To observe swimming currents, etc., suspensions of carmine and starch stained with iodine were employed.

In examining the structure of the appendages various methods were tried. Staining with acetic-alum-carmine, Bethe's old stain for chitin, and picro-nigrosin, showed the musculature and general features very beautifully, but the two last-named are difficult to control. Finally, it was found that the arrangement of spines and setæ could best be made out by comparing glycerine mounts of (*a*) fresh material; (*b*) material fixed in formalin-sea-water; and (*c*) similar material subsequently treated with alcoholic potash, a method which Hansen has recommended.

The arrangement of the mouth-parts was in part made out by dissection, and also by cutting thick sections of material embedded in

clove-oil-celloidin. This modification of Cannon's method was evolved by Mr. Dennell.

GENERAL BIOLOGY.

1. Habitat, Substratum and Salinity.

Though often occurring in great numbers, *C. volutator* has an exceedingly localised distribution. The unfortunate naturalist who is in need of specimens, and simply goes to the nearest estuarine mud-flat to find them, is likely to have a day's arduous search for nothing. With foul black mud, or Zostera, they will have nothing to do, but are to be found in certain areas of fairly soft greyish mud, when the other conditions are suitable.

A good description of a typical habitat for *C. volutator* has been given by Delage (**8**) in his work on the circulation of the Edriophthalma ; he says, " Corophium is found at Roscoff, in the mud of the harbour. They are not really very abundant except in an easily defined zone a little below the level of high-water neaps. At places where the mud is rendered black by abundance of decaying organic detritus, one never finds them." Stephensen (**20**) quotes Th. Mortensen to the effect that in company with the Spionid *Pygospio elegans* Claparède, Corophium is very numerous in certain areas of sandy mud in some of the Danish Fjords where the salinity is fairly low (*ca.* 6–16°/$_{oo}$). Finally, Gurney (**10**) has described *Corophium volutator* living in colonies of the hydroid Cordylophora, when ascending far up the East Anglian rivers into regions where the salinity is very slight.

Descriptions such as sandy mud, and mud not blackened by decaying organic matter, do not give sufficient information as to composition, and Dr. Orton suggested that it would be useful to give an accurate description of the mud which *C. volutator* normally inhabits. This I have attempted to do by the methods Allen (**1**) employed for grading bottom deposits.

The mud was passed through sieves with perforated zinc bottoms, the perforations being 5, 2·5, 1, and 0·5 mm. in diameter.

The portions retained by each sieve were dried on a filter paper, and later by gentle heat. Most of the mud passed through these sieves. Of the remainder, that which settled in the washing water in one minute was collected and dried, being equivalent to the " fine-sand " grade, and the residue in the water was left for 24 hours to settle, representing Allen's " Silt." The various fractions were carefully dried and weighed, and their percentage of the total sample calculated. Only in Whitby mud were the portions retained by the sieves an appreciable fraction of the total dry weight, and there they formed barely 9%. Accordingly in describing the different muds I have termed them collectively the " coarse grades," fine sand, and silt being spoken of as " fine grades."

Having obtained the dry weight of the various grades, the organic content was found by loss in weight on bunsen ignition (R. H. Worth, in **1**). I have not yet been able to carry out investigations of the carbonate content, for which blow-pipe ignition was needed. This is unfortunate as the pH of the muds is definitely on the alkaline side, *ca.* 8·2, which is surprising in view of the high organic content. In the course of this part of the work, it became very evident that an investigation of the physical factors of muddy foreshores, as influencing the organisms living on them, of the type recently worked out by J. R. Bruce (Journ. Mar. Biol. Assoc., XV, No. 2) for sandy beaches, would prove a very interesting and probably valuable study in itself.

Samples of mud from three different localities worked, Whitby, Salcombe and Calstock, have been analysed by the above methods, and the results, together with rough values for the salinity and frequency of Corophium in the different localities, are given in Tables I, II, and III.

Corophium is most abundant at Whitby (Table I), and is, moreover, the dominant species of the animal community of the mud there. In this mud there is a certain amount of shelly gravel, small stones and coarse sand, to the extent of nearly 9% of the dry weight, though some of this is due to large organic, mainly deciduous detritus, of the remaining 91%, 56% represents fine sand and 35% silt. The total organic content is 6·32% by weight. The coarse grades contain relatively twice as much organic matter as the fine grades. The salinity range appeared to be 21·8–35‰.

At Salcombe (Table II) Corophium is very scarce and this is probably due to the fact that the mud dries off almost completely at low tide, which is never the case where Corophium is plentiful. A titration gave 35·2‰ at half-flood (Corophium level in this Estuary). The mud on the whole is very similar to the Calstock sample, though the total organic content is not so high—only 7·08% by weight. The whole character of the mud is finer than the Whitby sample, as silt exceeds fine sand here by 12%.

At Calstock (Table III) the mud is finer still, and the organic content is higher, 10·41% by weight. It is therefore improbable that the texture of the mud is responsible for the scarcity of Corophium at Salcombe, as at Calstock it is fairly plentiful, *ca.* 40 individuals per sq. m. The cause of the disparity between the populations of these two localities is to be sought for in the almost complete drying-off of the mud at Salcombe. In the case of the relative frequency at Whitby (*ca.* 150 per m. sq.) and Calstock, I have no doubt that the difference is due to the texture and general character of the mud of the two localities. The coarser Whitby mud would allow of more rapid diffusion of oxygenated water by capillarity between its particles, and the Calstock mud, with its high organic content, is verging on the blackened condition in which, as Delage long ago pointed out, one never finds Corophium. It is true that the salinity at Calstock

must be appreciably lower than at Whitby. At Calstock a titration of flood-time water indicated 22·8°/$_{oo}$ as the upper limit of the range. But Corophium from any of the three localities would withstand great dilution under laboratory conditions, and it seems probable that only the extreme limit of tidal influence would prove to be the limit of their riverward extension in nature. A factor which must also be taken into account is the rate of evaporation during the intertidal period. Some of Bruce's results

Table I.

Analyses of Mud Inhabited by *Corophium volutator*.

Whitby.—W. side Harbour, opposite L. & N.E.R. Goods Yard.

Grade.	Dry wt. % of total sample. grm.	Org. cont. % by wt. of total sample. grm.	Org. cont. % of total organic wt. grm.
Retained by 5 mm. sieve	5·39	0·49	7·75
,, 2·5 mm. ,,	0·97	0·19	3·01
,, 1 mm. ,,	1·34	0·14	2·12
,, 0·5 mm. ,,	1·11	0·07	1·12
Settled in 1 min.	56·17	1·94	30·62
,, 24 hrs.	35·04	3·49	55·38

Total organic content % by wt. *6·32*

Coarse grades, gravel, shell fragments, large vegetable detritus, 8·788%.
Fine sand and silt, 91·312%.
Organic content of coarse grades, 10·13% by wt.
Organic content of fine grades, 5·08% by wt.
Corophium dominant, over 150 per sq. m., few small.
Nereis diversicolor etc., salinity 21·8–35 (?) °/$_{oo}$.

Table II.

Salcombe. Mud-flat between Ditchend and Southpool Lake.

Grade.	Dry wt. % of total sample. grm.	Org. cont. % by wt. of total sample. grm.	Org. cont. % of total organic wt. grm.
Retained by 5 mm. sieve	0·32	0·11	1·55
,, 2·5 mm. ,,	1·10	0·29	4·09
,, 1 mm. ,,	1·10	0·37	5·32
,, 0·5 mm. ,,	0·78	0·11	1·55
Settled in 1 min.	42·15	2·44	34·46
,, 24 hrs.	54·55	3·76	53·12

Total organic content % by wt., *7·08*

Coarse grades (mainly shell fragments and vegetable detritus), 3·40%.
Fine sand and silt, 96·60% by wt.
Organic content % by wt. of coarse grades, 25·88.
Organic content % by wt. of fine grades, 6·35.
Corophium scarce, less than 1 per sq. m. *Polychæta* (*Melinna adriatica* and Nereids) apparently dominant.
Salinity ebb-tide water 35·2°/$_{oo}$—conclude no dilution.

Table III.

Calstock. Cornish Bank of the R. Tamar, half a mile below Village.

Grade.	Dry wt. % of total sample. grm.	Org. cont. % by wt. of total sample. grm.	Org. cont. % of total organic wt. grm.
Retained by 5 mm. sieve	0·22	0·16	1·73
„ 2·5 mm. „	0·57	0·14	1·34
„ 1·0 mm. „	0·66	0·09	0·87
„ 0·5 mm. „	1·03	0·44	4·23
Settled in 1 min.	41·39	2·83	27·19
„ 24 hrs.	56·13	6·75	64·64

Total organic content % by wt., *10·41*

Coarse grades (vegetable detritus and gravel), 2·48% by wt.
Fine sand and silt, 97·52% by wt.
Organic content % by wt. of coarse grades, 33·46.
Organic content % by wt. of fine grades, 9·82.
Corophium fairly plentiful, *ca.* 40 per sq. m. *Nereis diversicolor* (large) dominant.
Salinity range must be great, *ca.* 0·8–16°/$_{oo}$ opposite Calstock itself (Percival, Jour. Mar. Biol. Assoc., Vol. XVI, 1929) on titration of flood-tide water gave 22·8°/$_{oo}$.

indicate that in the coarser mud evaporation would be less rapid. As before stated, Corophium is most plentiful where small puddles cover most of the mud at low water, and where the mud is relatively coarse. The most productive locality I have yet found for Corophium is in a certain tidal creek in the Salicornia marsh at Blakeney Point, Norfolk. Here the mud is very coarse, the salinity never less than 34°/$_{oo}$ and Corophium reaches a density of *ca.* 1000 per m. sq. Here also the organic content is very low (0·8% by weight). The inference is that the nature of the substratum, and not the salinity of the water, is the chief factor defining the habitat of this species of Corophium.

In this connection it is interesting to compare the remarks of Ussing (**22**) in a brief account of the biology of *Corophium Bonelli* M. Edw. in Mariagerfjord, E. Denmark. He found this animal to be the dominant species of a definite Epifauna (" Paa-fauna ") on the Mytilus clumps, and that it attains its optimum opposite Aamölle where the salinity is 14–15°/$_{oo}$ " just like its companion *C. grossipes* (=*C. volutator*) in Randers Fjord." From the above I can only conclude that the substratum was more suited to Corophium than that found higher up the estuaries I have worked. Only once I have found Corophium really abundant in a region of really low salinity—in the mouth of a small river in N. Norfolk connecting by faulty sluice-gates with a tidal creek, known locally as " Stukey Freshes." Here in July Corophium was as plentiful as at Whitby, though the salinity was only 0·7–3·6°/$_{oo}$. The mud was of about the same consistency as at Whitby, and organic content low. In September there was a heavy

accumulation of vegetable detritus, and the stream had to be cleared, but not before Corophium had rapidly diminished in numbers.

In addition to those I have worked myself, I have found records of *C. volutator* from the following British localities :—East Norfolk rivers, ascending to regions of very slight salinity living amongst Cordylophora (Gurney) ; very abundant in the Dee estuary (Spence Bate) ; Exmouth (Allen and Todd) ; tide pools near high water, Lytham–St. Anne's, Ribble estuary (Prof. Garstang).

An idea of the extent of its geographical range may be gathered from the following scattered references : in Christiana Fjord at Moss, G. O. Sars ; at Hangesand on the W. coast of Norway, Boeck ; Danish coasts, Stephensen ; Bohnslaa, Bruzelius ; Baltic, Lindstrom ; Kattegat, Meinert ; Dutch coast, Hoek ; coasts of France, Roscoff, Caen, Bernieres-sur-Mer, etc., Mercier and others ; Adriatic, Meller ; besides the various British localities.

G. O. Sars (**15**) dredged *C. volutator* in 2–5 fathoms of water in Christiana Fjord, whereas round our coasts it is always found in the intertidal zone. This is possibly an example of the general fact that species with a wide geographical distribution tend to be found in deeper water towards the polar limit of their range.

As regards the actual change in salinity which *C. volutator* can endure, it was found that starting with 40 c.c. of sea-water and adding 15 c.c. distilled water daily two Salcombe caught males showed no signs of inconvenience at the end of three weeks. In another experiment specimens from Salcombe were put straight into fresh water and specimens from Calstock straight into laboratory tank water (*ca.* 36‰). The experiment was set up on April 13th and had to be discontinued on the 29th. Almost all the individuals (two females and one male were used in each experiment) were still flourishing, but such young as were hatched apparently died at the first moult, and one of the Calstock females died after the eggs had hatched. If the salinity were changed gradually therefore, it seems reasonable to suppose that Corophium could be kept and bred in fresh water, and possibly even in hypertonic sea-water.

2. Burrowing and Locomotion.

C. volutator normally burrows vertically into the mud to a depth of not more than five inches. Frequently the burrows are U-shaped, having two openings. When kept in a dish with a shallow layer of mud, shallow burrows, perforce nearly horizontal, are formed. If the mud is insufficient even for this, they agglutinate it together in clumsy tubes, reminiscent of the more workmanlike structures of the regular tube-building species, *C. crassicorne*, with the aid of the secretion from the glands of the second

pereiopods, which is normally used merely to keep the walls of the burrows intact.

In burrowing, the large pediform second antennæ are first brought into play, and when these are immersed the gnathopods, and more particularly the first and second pairs of pereiopods, continue to enlarge the hole and haul the animal head-first into it, purchase being obtained by the elongated specialised fifth pereiopods. Additional drive is given by the continual beating of the abdominal pleopods and the bending of the abdomen under the body so that the uropod spines become embedded and propel the animal forward when the abdomen is straightened again. When crawling freely in the film of water on the surface of the mud *C. volutator* may progress slowly by scrambling action of the thoracic appendages and the beating of the pleopods, the first two pairs of pereiopods doing most of the work. A much more common method of progression, and one which is always used if the mud has dried off completely, might well be described as "looping." The second antennæ are lifted, thrust forward, and the first joint hooked into the mud. The animal hauls itself up to them like a ship kedging off a shoal, what time the abdomen is flexed ventrally so that when the animal straightens out for the next heave with the antennæ, it is thrust forward a further half of its length by the straightening of the abdomen. This mode of locomotion gives an effect very similar to that of a looper caterpillar, and the animal can progress quite fast by it. The structures concerned obviously lend themselves very efficiently to the process, the uropods with their short strong spines forming an ideal fulcrum.

When swimming clear of the bottom, the animal nearly always lies on its back, though capable of performing complicated evolutions on occasions, to which its specific name is possibly due. The two great second antennæ are laid back like the arms of a man about to dive, so serving as an admirable cut-water. All the other limbs are held stiff, with the exception, of course, of the pleopods. These beat rhythmically, but exactly out of phase with each other, i.e. with a metachronial rhythm. The basal joints of the fourth and fifth pereiopods are provided with a dense fringe of plumose setæ, which apparently helps to confine the current produced by the pleopod and direct it backwards, so propelling the animal forward. This mode of progression might be aptly compared to that of the early stern-wheel paddle-steamers.

3. Relations with Other Animals.

In the section on feeding habits, it is shown that *C. volutator* feeds mainly in vegetable detritus, and is *not* actively carnivorous preying upon small worms and gasteropods, as was formerly supposed.

In the Whitby mud it was the dominant species in the animal community. In addition to Corophium I found fair numbers of small *Nereis*

diversicolor and the small gasteropod *Paludestrina stagnalis*. Both these forms, in muds of a slightly different character, where Corophium is absent, may be present in countless thousands. In the Whitby mud were also a few small Lamellibranchs, probably *Tellina balthica*. Besides these, in the runnels there were a few small specimens of *Crangon vulgaris*, and in March I found some berried individuals of *Hippolyte varians*. Small shore crabs were occasionally present, also flounders, which come up on to the flats when the tide is up to feed on Corophium, and sometimes get stranded in small runnels. In the stomach of one small flounder I found 32 Corophium, and no doubt other fish take them on occasions. *C. salmonis*, one of the two large species described by Bradley (**5**) from the Pacific coast of North America, is found in large numbers in some of the salmon there.

At Salcombe the mud, though stiffer, was also stickier, and Corophium was scarce. Nereis and *Melinna adriatica*, which builds vertical tubes coming just above the surface of the mud, appeared to be dominant.

The Calstock mud was softer and darker than that at Whitby. Large *Nereis diversicolor* were dominant, and Corophium was fairly plentiful. I saw no signs of any other animals.

In the two localities worked at Blakeney Point, the salt-water "Yankee Creek" and the brackish "Stukey Freshes," Corophium was in both cases dominant though infinitely more abundant in the former. In "Yankee Creek" there were besides Corophium a large number of small *Nereis diversicolor*, but these were outnumbered five to one. A few *Tellina fragilis*, Carcinus, and *Crangon vulgaris* were also present. At "Stukey Freshes" other animals inhabiting the mud were *Nereis diversicolor* and the Isopods *Cyathura carinata* and *Sphæroma rugicauda*.

Besides fish, Corophium is preyed upon by wading birds and gulls. I have an original sketch by Mr. A. H. Patterson of Yarmouth of a wader with a Corophium struggling in its bill.

I have not as yet noted any parasites, apart from the fact that several of the Whitby Corophium had small individuals of Mytilus growing upon them. Presumably the spat, falling upon soft and unsuitable ground, finds in Corophium the best apology available for a hard substratum.

4. Feeding Habits.

Bate and Westwood (**2**) state that *C. volutator* attacks Annelids and Molluscs, the only other animals commonly occurring in the same mud. They give a "charming vignette" of the animal engaged in a mighty struggle with a Nereid, and state that combined assaults of such a nature are more common. However, they admit in their introduction that it is doubtful whether Corophium really does feed thus, and also admit the

improbability of the supposed migration of Corophium to deeper water in winter. Their accounts of these two phenomena are based on a letter from an early and obscure French naturalist to Latreille.

It seemed much more probable that like the majority of littoral Amphipoda, Corophium would feed on the organic detritus, mainly vegetable, present in its natural habitat. Before any attempt to study the actual feeding process was made, an experiment was set up with a view to determining this.

Small numbers of winter-caught Corophium were isolated in equal volumes of sea-water under various conditions. In the control, only the freshly filtered sea-water was present ; in another bowl mud was placed in which the organic matter had been destroyed by ignition ; another

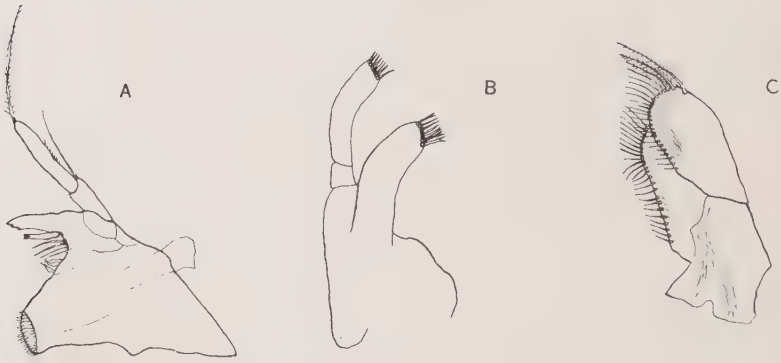

Fig. 1.—A, mandible ; B, 1st maxilla ; C, 2nd maxilla. × 120.

contained mud from which all large particles had been removed by passage through a 0·5 mm. sieve ; and in the last was mud direct from the natural habitat. By the end of a fortnight, the animals in the control experiment and with the sterilised mud were dead. Those with the sieved mud lived nearly 6 weeks, and those with natural mud were still flourishing nearly 7 weeks after the experiment had been set up, and made no attempt to molest the small molluscs present. It was thus obvious that *C. volutator* feeds on the organic detritus in the mud, together with the attendant micro-organisms, and investigations of the feeding mechanism were begun.

So far from being an active carnivorous feeder, then, *Corophium volutator* seems to feed almost entirely by selecting particles from the mud in which it lives. For this purpose the mouth-parts and gnathopods, particularly the first pair, are very well adapted. It would seem to be a true selective deposit feeder in Hunt's sense, though when in its burrow the current produced by the beating of the pleopod brings small particles

in suspension over the setæ fringing the gnathopod, so that in addition there is a filter-feeding mechanism. This last, however, is not the most important method of feeding, as nearly all the individuals examined had particles in the foregut, and adhering to the mouth-parts, of a size that are not moved by the current produced by the pleopods, even when this

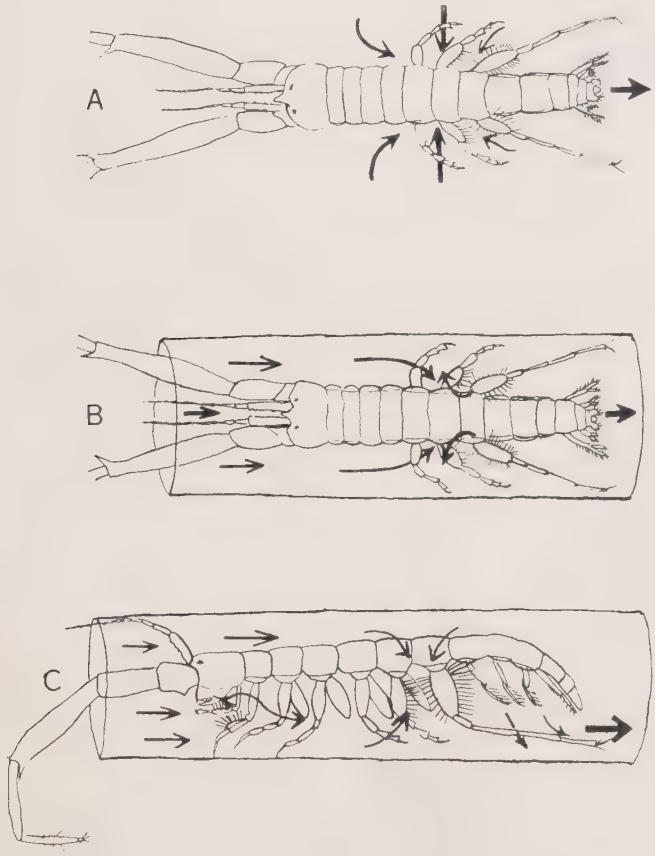

Fig. 2.—Diagrams showing the currents formed by Corophium. A, when crawling freely over the bottom; B and C, when enclosed in a tube.

current is concentrated by the walls of a tube. This can be proved by observing Corophium in a glass tube in a dish of water and adding mud from the natural habitat. Only the finest particles are carried in by the current. The confining influence of a tube is necessary for the filter-feeding mechanism to be operative at all. Otherwise the strong inflowing current is entirely lateral, as indicated in Figure 2.

By observation with a binocular microscope, of vigorous fresh-caught Corophium introduced into a glass tube as described above, the course of the currents, and the method of passing the particles caught to the inner mouth-parts can be followed (Fig. 2).

Before the feeding mechanism can be clearly explained it is necessary to give some account of the topography of the mouth-parts.

The labrum descends vertically from the extreme end of the head, and is provided with a row of small inwardly directed close set teeth near its inferior margin. On either side of the mouth-opening and immediately behind the labrum lie the mandibles. The incisor processes meet ventrally in close juxtaposition to the free edge of the labrum. The large molar processes are visible in sections at this level, lying deeper, i.e. nearer the mouth-opening proper, but their broad grinding surfaces are much wider than the incisors, and extend some distance further back in the plane of the long axis of the animal. The spinose ends of the plates of the first maxillæ overlap this backward extension of the mandibles. Overlying these ventrally come the setose plates of the second maxillæ, and outside these again are the maxillipeds, with the palps reaching as far forward as the labrum, to complete a sort of basket under the head of the animal opening forwards and inwards at the mouth (Figs. 1 and 4).

The mouth-opening itself is somewhat indefinite, lying buried beneath the molar processes of the mandibles. The paragnaths are scarcely developed at all, just two slightly raised blunt lobes with a fringe of fine short setæ, at the posterior end of the mouth-opening. Sections show the region of the mouth-opening and œsophagus to be richly supplied with glandular tissue.

When behaving as a selective deposit feeder, *C. volutator* crawls slowly about over the surface of the mud, or occasionally, on finding a patch rich in organic detritus, remains stationary while the feeding goes on. With the first gnathopods it scoops up and sifts small quantities of mud—when viewed laterally with the binocular the rain of rejected particles could clearly be seen. Larger fragments of algal detritus, etc., appeared to be conveyed to the incisor processes direct by the two terminal joints of the gnathopods. The smaller particles are retained in the fringe of the setæ on the fifth joint of the first gnathapods.

The larger food masses are not cut up by the incisor processes, which are manifestly unfitted for such a purpose, but are, as it were, tucked in between the molar processes by their action. The mandibles move laterally outwards and inwards as indicated in Figure 3, A. The particles are thrust in between the molars largely by the action of the laciniæ, and the spines that lie between them and the molars.

A considerable amount of secretion from the glands in the œsophageal wall is poured out into the cavity formed by the mouth-parts. Pear-

shaped masses of smaller food particles agglutinated together, are frequently found on the spines of the mandibles and first maxillæ.

When acting as a suspension feeder, the particles are drawn into the net formed by the fringing setæ of both first and second gnathopods, by the currents set up in the burrow (or glass tube) by the beating of the pleopods. The particles are combed out of the fringe of the second gnathopods on to the first gnathopod fringe, and their further course to the mouth is the same as that taken by the smaller particles obtained when deposit-feeding.

The transference of the smaller food particles from the setæ fringing the fifth joint of the first gnathopods to the mouth is not easy to follow, owing to the small size of the mouth-parts and the rapidity of their movements. Repeated observations of the animal fastened down upon its back with plasticine enabled the main part of the process to be made out.

The gnathopods are moved up and down against each other in the manner indicated in Figure 3, B, until the sifting of the useless particles appears to be completed to the animal's satisfaction. Even so, a large part of the gut contents can only be described as mud. One of the gnathopods is then inclined inwards so that by the rapid champing action of the maxillipeds the food particles are combed out of the setæ fringe on the gnathopod. The movement of the maxillipeds appears to be purely lateral, and the fringe of fine spines on the outer plate, together with those on the palp, appear to be the chief agents in collecting the food particles. The spines on the outer plate are so set in a sort of ball-and-socket joint that when the maxillipeds are closed, the joint admits of their being projected forwards at an angle, but not back. When the maxillipeds are opened laterally these spines are pointing inwards at right angles to the margin of the plate (Fig. 3, C), but when they close the spines bend forwards so that the food particles combed from the gnathopod fringe are thrust forward until they come within the radius of action of the incisor processes and first maxillæ (Fig. 3, C 2). It is possible that the armature of the second maxillæ functions in the same way as that of the maxillipeds, but the organs in question do not seem to play any important part in the feeding process.

The ends of the outer plates and palps of the first maxillæ move downwards and outwards, then upwards and inwards, and with the help of the secretion from the salivary glands, appear to do the bulk of the work of passing food particles on from the maxillipeds to the mandibles. Some of the larger particles, however, seemed to be passed direct to the inner side of the incisor processes by the palps of the maxillipeds.

Most of the food seems to be ground up into a pasty mass by the molar processes, but some particles, particularly fragments of algal filaments, appear to reach the fore-gut without undergoing this trituration.

The actual process of swallowing is not at all clear, but it seems probable

that suction set up by contraction of the diagonal muscles of the foregut wall may be the chief factor. The dilated horizontal part of the foregut or crop contains an exceedingly complicated arrangement of spines,

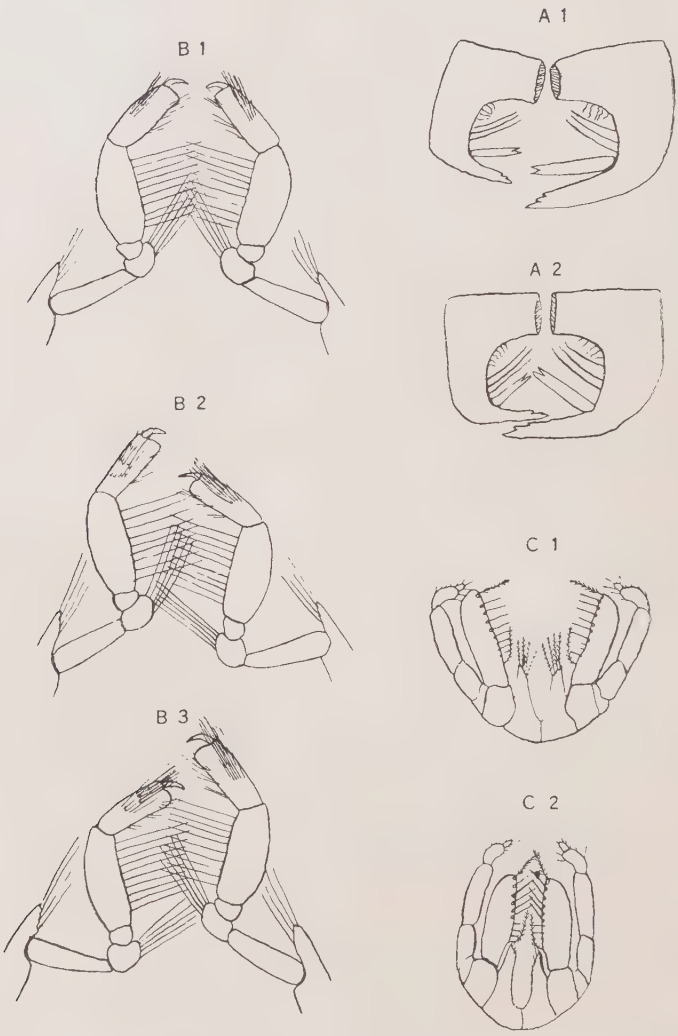

FIG. 3.—Diagrams illustrating the feeding mechanism. A, action of the mandibles; B, sifting action of the first gnathopods; C, action of the spines on the maxillipeds.

denticles and setæ, by means of which the undigested food is still further triturated. Obviously this can only take place by the action of the muscles in the wall of the crop, and it seems quite probable that this same action

sets up a suction by means of which further food particles are drawn up the œsophagus.

The œsophagus ascends almost vertically into the wide triturating stomach or crop (also sometimes termed the proventriculus) which projects anteriorly in front of the level of the mouth-opening. The forward end of the crop contains a circular ring of chitin set with strong backwardly directed triangular teeth, the "triturationsapparat" of German authors, at the level of the œsophageal opening. Just behind this is a ring set with numerous fine setæ, also directed backwards.

Further back a large ridge rises from the floor of the fore-gut and almost divides it longitudinally into two halves. This ridge is set with a fur of very fine short setæ round the crest, and on the sides with parallel rows

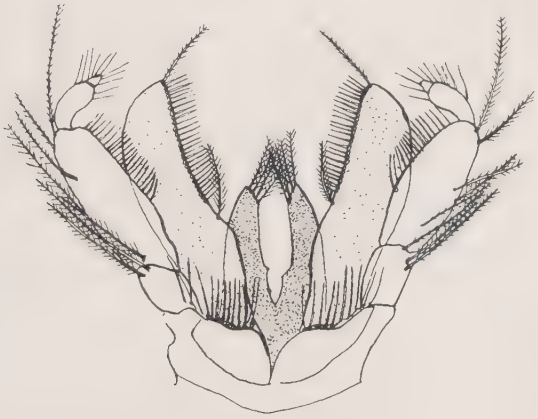

Fig. 4.—Maxillipeds, as seen from below. × 120.

of low chitinous denticles. At the extreme postero-dorsal end, the ridge also bears a tuft of longer setæ directed backwards. The armature of the ridge in general closely resembles that of the molar processes of the mandibles. On either side, where the lateral walls of the fore-gut join the floor, a low ridge is to be found directed obliquely inwards, crowned with fine short setæ. The whole apparatus will obviously furnish a very efficient triturating apparatus when the gut walls are violently contracted. These walls contain many strong diagonally interlacing muscle-bands, giving an appearance reminiscent of the network of a balloon. Behind the proventriculus the gut narrows abruptly, but the fore-gut is prolonged as a sort of funnel for some distance into the mid-gut lumen.

Little could be seen of the actual mastication of food within the proventriculus in the adult, for obvious reasons, but in young transparent individuals a violent periodic lateral contraction, followed by peristaltic

movement of food down the mid-gut, could clearly be seen. These spasmodic contractions were always followed by the appearance of a fresh supply of food particles in the proventriculus. Hence, I incline to the view that the swallowing process is to be attributed to the sucking action of the crop.

5. Life-Cycle and Breeding Habits.

Results of Measurement Investigations.

Samples from 1 sq. m. of the Whitby mud were taken at the four seasons of the year, by the methods described earlier in this paper. All the measurements were made by Blegvad's method—taking the length in millimetres from telson to rostrum: and in the case of the females, the condition of the oostegites, and eggs or young if present, was carefully examined in each individual as it was measured.

The smallest individuals in which the sexes could be distinguished with any degree of certainty without dissecting off the antennæ were about 3 mm. long. In some of these, though the oostegites were not developed, the two spines on the inferior margin of the first joint of the first antennæ, so characteristic of the females, could clearly be seen. This is a most constant secondary sexual character in all the material I have examined. All specimens below this size are lumped together as "young" in the following tables. As many of them doubtless escaped the mesh their numbers have little significance, apart from their relative frequency at midsummer, when the animals are breeding, and through autumn and winter when breeding has ceased but development is very slow: and scarcity in the spring, when the last hatched broods of the previous summer are just reaching maturity, and the animals are about to begin breeding again.

Table IV deals with the sample of *Corophium volutator* obtained from 1 sq. m. of Whitby mud on July 20th, 1928. In addition to the tabulated specimens, this sample contained 53 young under 3 mm. in length. It will be seen that immature specimens of both sexes are almost entirely lacking, from which it would seem that the first brood of the year had just reached maturity. From the measurements given it also appears that maturity is reached at a length of *ca.* 5·5 mm. in the case of the summer stock. In the great majority of the larger females the eggs were in the same advanced stage of development. I take it that this shows the free-living young of the July sample to be representative of the second or third brood of the year, as information gathered during the following April points to three weeks as the maximum period of incubation, and breeding commenced in the second week of that month.

From the figures given in Table IV it will be seen that quite a large proportion of the 7 mm. females were without eggs, but had the brood

pouch fully formed. It would seem that these represent the last of the winter stock to reach maturity, and they had probably only produced one brood when taken. The validity of this supposition is greatly enhanced when the March measurements (shortly to be described) are taken into account.

Table IV.

Results of Measurement Investigations.

Whitby sample. July 20th, 1928.

Total number of individuals examined, 196, of which 55 were young under 3 mm. in length, 73 females ranging from 5–9·5 mm., 35 males varying between 6–9·5 mm. in length, and 33 females not so fully examined of length 5–8 mm. The first series shows the information gathered from the females examined in detail.

Length mm. telson to rostrum.	No. of individuals.	No. with eggs.	No. without eggs, but brood pouch present.	No. having eggs with curled embryos.	Max. no. of eggs per brood.	Min. eggs per brood.	Average no. of eggs per brood.
5	1	–	–	–	–	–	–
5·5	3	2	–	2	8	4	6
6	3	2	1	2	12	9	10·5
6·5	10	8	2	6	35	11	25
7	22	13	9	12	39	24	28·7
7·5	15	11	4	10	48	25	33
8	13	11	2	11	45	21	34·5
8·5	3	2	1	2	39	32	35·5
9	1	–	1	–	–	–	–
9·5	1	–	1	–	–	–	–
Particulars from 33 more females, not so closely examined.							
5	2	–	–				
5·5	1	–	–				
6	3	2	1				
6·5	4	4	–				
7	14	10	4				
7·5	4	4	–				
8	2	1	1				

Table V.

Size and Frequency of the July Males.

Length in mm. telson to rostrum	6	6·5	7	7·5	8	8·5	9	9·5
No. of individuals	1	2	10	8	7	5	–	1

Table VI shows the measurements of the sample taken on October 10th, 1928. The scarcity of adults, particularly males, and larger immature stages, together with the increased proportion of free-living young was very marked. None of the larger females had eggs ; indeed, it was found that the hairs were missing from the oostegites, which showed notches where the hairs are present during the breeding season. This was borne out by examination of some forty individuals apart from those in the mature sample. My opinion is that the apparent scarcity of *C. volutator* during the autumn and winter months is not due to any migration into

deeper water as was suggested by Bate and Westwood (2), but to two main factors: firstly, that the adults, in particular the males, are dying off rapidly; secondly, that small free-living young, which do not become mature until the following spring, are exceedingly numerous, but defy ordinary methods of capture.

Table VI.

Results of Measurement Investigations.

Size and frequency of the Whitby sample obtained on October 10th, 1928. *N.B.* A 500 c.c. sample put through a finer sieve yielded 33 young. The females were not breeding.

Length in mm. telson to rostrum.	Nos. of Females.	Nos. of Males.	Young.
Under 3	–	–	21
3	12	–	–
4	6	–	–
5	4	–	–
6	3	–	
7	12	1	
8	1	1	

The total number of individuals examined was 64, of which 41 were females, 2 males and 21 young.

Table VII.

Measurements of a sample obtained at Whitby on December 29th, 1928. Only 60 individuals were found, of which 51 were females, mostly immature, 3 were males, and 6 young. A 500 c.c. sample put through a fine sieve again indicated that many young had escaped the larger mesh, as 14 young were found in it.

Length in mm. telson to rostrum.	Nos. of Females.	Nos. of Males.	Nos. of Young.
Under 3	–	–	6
3	12	–	–
4	18	1	–
5	7	–	–
6	6	–	
7	4	1	
8	4	1	

In order to prove that Corophium is not so scarce in October as the metre sample indicated, a sample of 500 c.c. of mud was put through a fine sieve in the laboratory, when 33 young were discovered. As this volume only represents about 1/20th of the metre sample, it will be seen that the scarcity of Corophium in the autumn is confined to the adults and larger immature stages. The occurrence of a fair number of individuals 7 mm. long or over shows that the adults of the previous summer had not completely died off, as one would expect thus early in the "off-season."

In the sample obtained on December 29th, 1928, the number of adults was still smaller, and the number of free-living young in 500 c.c. of mud had decreased to 14; but the number of small immature stages was considerably greater, as shown in Table VII. No breeding animals were

observed, though 21 large females apart from the sample were examined. Their oostegites were hairless, with notches where the hairs are found in the breeding season.

The last sample I have so far been able to take at Whitby was collected on March 28th, 1929 (Tables VIII and IX). The wintered females were obviously almost ready to breed, but though 107 in all were subjected to the closest scrutiny, not one was discovered actually breeding. Indeed, their oostegites were still hairless, even in the larger individuals, but were not notched as are those of the mature females of the previous summer which live on into the winter. All the latter seemed to have died off.

The following Tables VIII and IX show the results obtained from the metre sample taken at Whitby on March 28th, 1929. The males which are dealt with were more numerous than at any other time of the year. In all, this sample contained 184 specimens, of which 5 only were young under 3 mm. long, 70 were males ranging from 4–8·5 mm. in length, and 107 females of length 3–8 mm., none of which were breeding. A 500 c.c. sample put through a fine sieve did not yield any young, but 20 immature specimens of both sexes, from 4–6 mm. in length.

Table VIII.

Length in mm. telson to rostrum	4	4·5	5	5·5	6	6·5	7	7·5	8	8·5
Nos. of males	2	4	9	10	24	7	9	1	3	1

Table IX.

The females showed all stages of development of the oostegites, but in general, the larger the individuals the more advanced was this development, as shown below :—

Length in mm. telson to rostrum.	Nos. of Females.	Nos. without oostegites.	Oostegites small or vestigeal.	Oostegites well developed but hairless.
3	10	10	–	–
3·5	9	9	–	–
4	11	10	1	–
4·5	14	3	11	–
5	15	3	11	–
5·5	9	–	3	6
6	9	–	–	9
7	11	–	–	11
7·5	7	–	–	7
8	1	–	–	1

The first vestiges of oostegites were observed on females 4·5 mm. long. Larger females, of a size commonly found breeding in the summer, had well-developed oostegites, but these were hairless. It would seem, therefore, that not only is the growth of the winter stock slower than that of the summer stock, but that they also reach maturity at a greater size.

An additional small supply of Whitby material, captured on April 10th,

and very kindly sent to me by Mr. George Duke of Robin Hood's Bay, showed that all the females were then developing hairy oostegites, and some had early eggs. The early eggs of *C. volutator* are easily distinguished from those at a later stage of development, as they are smaller, of a bright golden yellow colour, and held together by a viscid secretion.

On April 13th at Calstock, I found all the female Corophium breeding, mostly with eggs in this early stage.

Free-living young were scarce, so that it seems that even on the South coast they do not start breeding until April.

A few specimens of *C. crassicorne* dredged from Plymouth Sound about this time had advanced eggs, but it is quite possible that this species, like the closely similar *C. Bonelli*, breeds all the year round, as living below low water it will not have to cope with such great fluctuations of temperature as *C. volutator*.

Isolations of females with early eggs showed the probable time of incubation to be slightly over a fortnight, and this was borne out by a further sample from Whitby very kindly obtained for me by Mr. Wight on April 19th. This sample contained females nearly all of which had eggs at an advanced stage, whereas it was known that breeding had only just commenced at Whitby on April 10th. The first young were hatched on April 23rd, and by the 29th some were being extruded from the brood pouches. I have not yet been able to observe the mating of the *C. volutator* in captivity, so I am forced to rely on this indirect evidence, and can therefore only give an approximation of the incubation period at present.

The young remain at least five days in the brood pouch. They feed in it, for their guts can plainly be seen full of food, and at least the first moult must normally take place there.

The relative number of males was much higher in the spring sample than in the summer and, as before stated, adult males had become exceedingly scarce by October. From this it would seem that the earlier broods must contain many more males than those hatched in spring and early summer.

The conclusion arrived at from the above evidence concerning the life-cycle of *Corophium volutator* at Whitby were as follows :—

The breeding period lasts from April to September : several broods are hatched each year.

The last hatched broods mature slowly through the autumn and winter, and commence breeding in the following April. During autumn and winter the individuals which had reached maturity in the previous summer die off.

The species is thus annual or semi-annual.

The Young.

The young of *C. volutator* are hatched with the full complement of adult appendages, as is the rule amongst the Gammaridea. The primary flagellum of the first antennæ consists of but three joints, instead of four, as Sexton (**17**) found in several species of Gammarus. The proportions of both pairs of antennæ to the rest of the body are very different from that of the adult. In the young the second antennæ are never more than one-third of the body-length, and the minute terminal flagellar joint of the adult is wanting. The armature of spines and setæ of several of the appendages is poorly developed or wanting in the young. Thus only a few of the large plumose setæ on the gnathopods are represented, and these appear as long spines of totally disproportionate size to the limb bearing them, and on which I have not been able to discern any accessory hairs. The fringe of plumose setæ on the basipodite of the 5th pereiopod is entirely wanting.

The form and proportions of the regions of the body in the young also differ from the adult. The general form is shorter and squatter, and the ventral flexure of the abdomen is more marked. The abdomen is also much larger in proportion to the rest of the body.

The epipodites are already present, as would be expected, for though remaining in the brood pouch for at least five days, during which time the first ecdysis takes place, the young are quite active, and feed within the pouch. This has also been observed in the young of Gammarus by Sexton (**16**). If dislodged they appear to be quite able to fend for themselves, but the first moult is a critical period, and in experiments in varying the salinity it was frequently found that under conditions which did not affect the adults adversely, all the young died at the first moult.

In some of the young taken from the brood pouch, probably after the first moult, a single large spine was present, directed obliquely forward from the basal joint of the fourth antennæ ventrally. Further study may show this to be the forerunner of the two spines characteristic of the immature and adult females. If this is so, *Corophium volutator* will be the only Amphipod so far studied in which the sexes can be distinguished at such an early stage.

DISCUSSION AND SUMMARY

The investigation of the habitat shows that the nature of the substratum is the chief factor influencing the distribution of *Corophium volutator* in this country. The accounts of Danish workers state that it reaches its optimum in regions of fairly low salinity. This is probably due to the fact that the mud is of suitable character higher up the vast estuarine areas of Denmark than it is in England. It has been shown that while Corophium

can penetrate into regions of very slight salinity, it occurred in by far the greatest numbers at the "Yankee Creek" station, at Blakeney Point, Norfolk, where the mud is very coarse, the organic content low, and the salinity rarely falls below that of the North Sea outside. At "Stukey Freshes," also at Blakeney Point, Corophium was found in considerable abundance in July, although the salinity was very low (3·6°/$_{oo}$). At this time the organic content of the mud was 6·3% and the pH 8·3. In early September there was a vast accumulation of organic detritus at this station, and the pH was found to be 7·7. The numbers of Corophium present dwindled rapidly.

The conclusion reached is that while *Corophium volutator* is capable of withstanding great salinity change, its abundant occurrence is strictly limited by the chemical and physical character of the substratum.

The peculiar features of the structure of this Amphipod and its appendages, and the methods of feeding and locomotion to which these lead, are obviously of great advantage to an animal of its peculiar way of life.

C. volutator is a characteristic member of a definite type of animal community of which the other important forms are Nereid worms and the Gasteropod *Paludestrina stagnalis*. Where the conditions approach its optimum, *C. volutator* forms the dominant species in this community, but it is also found in fair numbers in regions where Nereids become dominant. Danish writers also speak of it as occurring in immense numbers co-dominant with the Spionid *Pygospio elegans*.

In describing the Biology of the allied species, *C. Bonelli*, Ussing (**22**) mentions that this form also is a characterising species of a definite animal community. This is the well-marked Epifauna of the Mytilus clusters in certain Danish Fjords. Salinity would appear to be the chief factor influencing the distribution of this species, and where the conditions depart from its optimum, other members of the Epifauna become correspondingly more numerous.

As regards the feeding habits of *C. volutator*, the method of selective deposit feeding appeared to me much more important than suspension feeding. The method of dealing with the larger food masses recalls that described by Cannon and Manton (**7**) in *Hemimysis lamornæ*, where large food masses are conveyed to the maxillules and incisor processes by the endites of the anterior thoracic limbs. In the Decapod, *Leander serratus*, large particles are dealt with by the chelipeds according to Borradaile (**4**), but the scooping up and sifting of the ooze by the gnathapods of Corophium finds a still closer parallel in the almost identical performance of the third maxillipeds of Hermit crabs (Orton, **13**).

The suspension feeding when the animal is in its burrow, by means of the current set up by the pleopods, agrees almost exactly with the description given by Hunt (**11**) in the case of another Amphipod, Ampelisca.

The actual swallowing action I could not definitely make out, but the reasons given for the suggestion that suction from the crop is the prime factor seem fairly sound. Parker and Mocquard have suggested a similar cause in Decapoda, but Borradaile (**4**) considers this doubtful, and suggests that the constrictor muscles of the œsophagus may conduct the process. The shortness of the latter organ in Corophium would seem to render such an explanation inapplicable in this case.

The life-cycle of *Corophium volutator*, as deduced from the measurement-investigations of Whitby material, would seem to be essentially similar to that postulated by Blegvad (**3**) for several littoral Amphipoda of widely different genera: but the wintering period, when the animals are not breeding, is much longer. Most of the animals discussed by Blegvad stopped breeding in October, but began again in the following January. Further, it seemed that none of the wintering adult individuals lived long enough to start breeding again in the following spring, though the numbers so far studied are not sufficient to permit of so much stress being laid on this point at present. It has been clearly shown, however, that wintering adult females lose the hairs on their oostegites, and it would be extremely interesting to observe the re-development of these, if they did breed again. Mrs. Sexton drew my attention to the very interesting work of Unwin (**21**) on the isopod Asellus in this connection. In this animal it seems that the oostegites remain inconspicuous until the ecdysis accompanying fertilisation, when they expand to form large brood-plates. Soon after the escape of the young, the female goes through another ecdysis, and the large oostegites are replaced by smaller processes. However, I do not think any similar phenomenon occurs in Corophium, as the lamellæ of the oostegites develop gradually as in other Amphipoda —the March sample showed females with the oostegites in all stages of development, becoming more advanced with increased size of the female (Table VIII). It is only the hairs that develop suddenly. Once present these hairs seem to remain until the end of the breeding season, as many females of the summer stock had fully developed brood pouches long after all the young had been extruded.

The fact that the breeding period of *Corophium volutator* is comparatively short for an amphipod is rather surprising in view of Ussing's observation that *C. Bonelli* breeds all the year round in certain Danish Fjords (**22**). The explanation is probably to be found in the fact that *C. Bonelli* lives on the Mytilus clusters just below low-tide mark and is therefore subject to much more uniform temperature conditions than *C. volutator*, dwelling on exposed flats which dry off every tide.

The fact that females are more numerous than males was known to Delage (**8**), and he gives the sex ratio as 3 : 1. This was precisely what I found at midsummer, but in March males were much more frequent,

though still outnumbered by the females. I am at a loss to account for this, unless the last hatched broods each year contain a much greater proportion of males than the others. If this were the case, it might be that a detailed study of the development of *C. volutator* would throw light on problems of sex determination.

The extremely slow growth of the young during the winter is also exhibited in a lesser degree by *Gammarus chevreuxi*, a species which, under aquarium conditions at any rate, breeds all the year round. Of this species Sexton (Journ. Mar. Biol. Assoc., XV, 1928, p. 40) says : " The rate of development is affected to a large degree by temperature and to a lesser degree by the seasonal rhythm. Young hatched in the winter months take longer to reach maturity, even though the temperature be raised to summer conditions, than those hatched in the spring and summer." Bearing in mind what happens in *C. volutator*, it seems at least possible that this " seasonal rhythm " may be due simply to the cumulative temperature effect on thousands of generations of these brackish-water amphipods, under natural conditions.

Note on the Morphology of the Gut Diverticula.

In the course of this study of *Corophium volutator* it was discovered that the anterior dorsal gut diverticulum was bifid, but that small posterior diverticula of typical Gammaridean character were present. The dorsal diverticulum should be single in all Gammaridea, but paired in Hyperiidea and Caprellidea, according to all authorities whose works I have been able to consult. Thus Calman (**6**), Della Valle (**9**) and others.

This is interesting in view of the fact that Delage (**8**) advances the hypothesis that Corophium represents the common ancestral stock of the Caprellidea on the one hand, and the Gammaridea on the other. His view is based on a minute examination of the circulatory system of most of the main types of the old group Edriophthalma, including this particular species of Corophium. Stebbing, however, disposes of this view very effectively (**18**), arguing on general lines. But the bifid nature of the " Nackendrüse," unique among the Gammaridea so far as I have been able to ascertain, seems at first sight to lend support to Delage's view.

While Stebbing's arguments would seem to preclude the possibility of Corophium being the direct ancestor of the Caprellidea, the singly ostiate heart of Corophium, and the bifid nature of the " Nackendrüse " certainly seem to point to some sort of affinity. In this connection the evidence furnished by this disposition of the other gut diverticula in Corophium may be considered.

In the first place, Corophium is provided with a pair of posterior gut diverticula. Baldwin Spencer (**17**) has pointed out the extraordinarily

limited occurrence of these organs among higher Crustacea, though Claus has described somewhat similar organs in Copepoda. They are almost entirely confined to the Amphipoda Gammaridea, being only exceptionally present (Calman, **6**) in Caprellidea and Hyperiidea. As Della Valle has pointed out, these organs are small in Corophium, but they are quite well developed, and agree with those of the more typical Gammaridea, as described by Wrzesniowski (**23**) in structure. The presence of these organs in Corophium is a serious objection to the hypothesis that the animal represents the common ancestral stock of the Gammaridea and Caprellidea by different lines of descent, as if this were the case one would have to postulate their gradual suppression in the latter group, whereas typical Gammaridean forms (e.g. Melita) are known in which the posterior gut diverticula are partially suppressed.

Corophium is not alone among the Gammaridea in having only one pair of hepato-pancreatic diverticula, though two pairs are more usual. In Caprellidea there is one pair only, but according to Calman (**6**) it is the ventrally situated pair which is rudimentary or absent, while in Corophium the well-developed hepato-pancreatic diverticula can clearly be seen to open into the mid-gut ventrally, and indeed are rather ventrally inclined to it throughout their length. Again, the evidence furnished by these organs in Corophium is in contradiction to Delage's hypothesis.

Taking all these facts into consideration, together with Stebbing's strong argument for regarding the Gammarus type as primitive, I suggest the substitution of the following for Delage's hypothesis : that Corophium is a secondarily modified amphipod, probably derived as an early independent offshoot from the evolutional series which started from Gammaridean stock, and culminated in the degraded Caprellids. On this view it is only necessary to suppose that the two anterior pairs of ostia, poorly developed in Caprellids, have disappeared altogether in the side line which gave rise to Corophium, while the balance of evidence gained from the disposition of the various gut diverticula is also maintained.

Note on a Variation of *Corophium volutator*.

In the female of this species, the first peduncular joint of the first antenna bears ventrally typically two stout spines direct obliquely forwards. Occasionally there are three or more of these spines either on one or both of the antennæ, as has been pointed out by Mercier (**12**), though I have never come across any similar spines in the male such as he also describes as varying in number. It is perhaps significant that Poisson and Legueux (**14**), in describing a variety of another Corophium species from the same locality, make no reference to any male spines in an otherwise rather full summary of Mercier's work. In the female, however, his

account of the variation is certainly correct, though the further conclusions are somewhat doubtful. The number of individuals with more than the normal number of spines is said to be higher in brackish than in salt water, and it is claimed that this phenomenon "doivent rentrer dans la cadre de variation de place."

The numbers upon which Mercier's observations are based are very small, and he makes no mention of the time of year at which collections were made. As far as I can say at present, it appears that this variation is not due to differing salinity, but rather to some factor correlated with the much higher rate of metabolism of the summer stock. These may take no more than two months to reach maturity while the winter stock take six. Of 103 females of the summer stock, 25 showed the variation in a more or less marked degree, while 109 of the winter stock contained only 3 variants. Further, these samples, from the sample locality at Whitby, came from a place where it appears that salinity rarely falls below *ca.* 20°/$_{oo}$.

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By

H. W. Harvey, M.A.,

Hydrographer at the Plymouth Laboratory.

With 16 Figures in the Text.

The temperature of the sea and the movements of water carrying with it planktonic organisms have been the subject of study since the early days of marine biological research. As investigation of cold-blooded marine animals progresses, the controlling rôle played by the temperature of the surrounding water upon their breeding, rate of growth, and general metabolism, becomes increasingly evident.

From 1902 to 1909 cruises were made throughout the English Channel by the s.s. *Huxley* four times each year, and from the data so obtained Matthews (1905–11) described the distribution of temperature at these times, as well as the distribution of salinity, and from these the general water movements were deduced. Conditions at the same time of year differed from one year to another. It was concluded that fluctuations from year to year in the annual temperature cycle and fluctuations in the inflow of water from the Atlantic would have a profound influence upon the population of marine animals and upon the fisheries. This conclusion has been borne out in this area notably by the researches of Orton (1920) upon the narrow temperature limits in which various marine animals breed, and of Ford (1929) upon the shoaling of herring for breeding purposes.

Since 1921 more frequent but less extensive cruises have been made by the s.s. *Salpa*, while surface temperature samples have been collected at intervals of about two weeks by cross-Channel steamers (see Fig. 1) for the Ministry of Agriculture and Fisheries, with the exception of the route Land's End to Ushant, on which data are collected for the Marine Biological Association. These surface data are published in the annual *Bulletin Hydrographique* of the International Council for the Exploration of the Sea. Hydrographic cruises have also been made to the west and south-west of the entrance to the Channel by French and Irish fishery research vessels, the data being published in the *Rapport Atlantique*. These data so collected throw light upon the fluctuations which have

occurred from year to year in both the movement of the water masses and in the annual cycle of temperature.

PART I. TEMPERATURE DISTRIBUTION.

The Annual Cycle.

The annual variation, or temperature cycle, differs from place to place and from time to time with the extent to which the surface layers mix with the water below, and with the depth or mass of water which is heated in summer and is cooled in winter. Further, the cycle fluctuates from year to year owing to fluctuating meteorological conditions, and on occasions owing to the inflow of water from other parts.

In shallow areas, where wave motion and turbulence due to tidal streams keep the upper layers mixed with the water below and in consequence keep the temperature nearly constant from top to bottom, the water commences to rise in temperature about a month before the vernal equinox and attains a maximum in the late summer. Such is found, for instance, in Plymouth Sound and in the shallow eastern part of the English Channel.

In the deeper waters of the Channel it is otherwise.

There is now a considerable body of data concerning the temperature cycle at Station E_1 (50° 02′ N., 4° 22′ W.) in a depth of around 71 metres. Here convection currents, wave motion, and vertical mixing set up by tidal streaming are effective in keeping the temperature almost the same from top to bottom during the winter. Later, as the water warms, receiving heat from solar radiation at the surface, there comes a time in May, June or July when heat arrives more rapidly at a depth of about 16 to 20 metres than the turbulent eddy motion of the water can carry it to greater depths. The resulting difference in density, between this upper warmed layer or epithalassa and the water below, still further damps down eddy motion at the discontinuity layer. Heat can only pass slowly through it to the water below. From this discontinuity layer to the bottom the water remains more or less isothermal, because tidal streaming over the bottom sets up eddy motion which is sufficient to pass downwards the heat which is arriving from the epithalassa.

Figure 2 shows the distribution of temperature which had been attained on August 2nd and 3rd, 1927, at Stations E_1 and E_3, 74 and 106 metres deep respectively.

Between 15 and 20 metres there is a sharp change in density, and in consequence considerable work must be done if the lighter water above is to mix with the heavier water below (Atkins, 1925). Vertical movement of water particles is tolerably free to take place between the surface and 10 or 15 metres. Hence heat from solar radiation, which is absorbed near

the surface, is freely passed on downwards from water particle to water particle to this depth by the eddying movements of the particles themselves, brought about by wave motion and the convection currents set up by cooling at night. If it were not for this mixing of the water particles carrying heat just as they carry momentum, and passing it on as in a relay race in the course of their eddy movements, the layering would be much shallower and higher temperatures would be attained near the surface, as happens in still water.

In the discontinuity layer the interchange or mixing of the water particles and their eddy movements are restrained. Hence momentum is not freely passed downwards, and this upper stratum is relatively free to slip horizontally over the heavier water, the slip taking place at the discontinuity layer. This undoubtedly takes place. At Station E_1 the water swings to and fro up and down Channel with the tides from the surface to near the bottom ; it appears that it does not swing to and fro as a whole body, but at times the upper stratum is travelling faster and slipping over the heavier water. A series of observations indicated also that the discontinuity layer oscillates vertically up and down to a slight extent.

Although the upper stratum is distinct, the many series of observations made at E_1 do not show sharp differences in salinity between this epithalassa and the heavier water ; there is no reason to suppose that the warm upper stratum flows in from other areas to cover the cooler water, yet summer land drainage doubtless flows out freely to mix with the upper stratum rather than diluting the deeper water. When an inflow of water into the E_1 area occurs during the summer, it is sometimes the case that high salinity water creeps in along the bottom.

Usually some time in August, as the intensity of solar radiation wanes, there is a gradual cooling of the upper warm layer, heat being lost from the surface by evaporation, by radiation outwards, particularly at night, and by gradual passage through the discontinuity layer into the cooler water below. Convection currents set up by loss of heat from the surface penetrate deeper and deeper, until finally the layering breaks down, often hastened by a gale, and isothermal conditions result.

At this time, usually in September or October, the deep water attains its maximum temperature (Fig. 3) unless, as happened in 1921, a mass of warmer water flows in from a neighbouring area.

During October and November the loss of heat from the mixed water is rapid. An analysis of factors leads to the inference that evaporation from the surface plays a major part in regulating the rate of cooling. During these two months in particular the vapour pressure of the relatively warm surface water exceeds the pressure of aqueous vapour in the

atmosphere (Harvey, 1925). By February or the beginning of March the minimum temperature is reached and the annual cycle completed.

While the formation of an upper warm layer is taking place in the open sea, every variant up to isothermal distribution with depth occurs as the shore or shallow areas are approached. Observations made on the line between Station E_1 and Plymouth on August 7th, 1924, reproduced in Figure 4 show this very clearly.

The water in Plymouth Sound is in connection with the large body of water in the Channel which tends to stabilise its temperature. On plotting the temperatures observed near the western end of Plymouth Breakwater, they are seen to be a little lower during the height of summer than the surface temperatures at E_1, vertical mixing being more active, and distinctly lower than the temperatures at the Varne Light vessel in the Straits of Dover, the centre of an extensive area under 40 metres in depth.

During the winter, inshore and shallower water temperatures are lower than in deep areas, similar heat losses having greater effect on shallower depths. The observations on January 7th, 1929, shown in Figure 4, illustrate this, as also the crosses in Figure 3. At the Varne Light vessel the winter temperatures are still lower. It is a fair generalisation that the annual range of temperature is greater the shallower the water and the less interchange taking place with the deeper open sea.

Surface Temperatures.

The surface temperature of the sea is usually taken from a sample drawn in a bucket and is usually taken as representative of the upper 4 to 6 inches. On a cloudy day or with a strong breeze there is rarely any distinct difference from the temperature at 5 metres, but with a clear sky during the afternoon in summer or after a frosty night in winter with a smooth sea the difference may be material, although unusual in this area. The matter is of some importance since a very great quantity of surface temperature data have been accumulated for the English Channel and North Sea, and from these charts can be drawn for the whole body of water during the winter months when isothermal conditions are known to exist. During the summer months the temperature of the upper 5 metres is so dependent upon vertical mixing due to wind, that such charts would have restricted value, except in the shallower areas, such as the eastern part of the English Channel, where vertical mixing overcomes the tendency towards layering. In view of this Table I has been compiled in order to give an idea of the source of error likely to arise in using surface temperature data. All the observations were made at about midday, while if they

had been made in the early morning doubtless some of the differences might have been greater; on the other hand, they were made on days when the sea was slight or moderate, while if the sea had been moderate or rough the differences would have been less.

TABLE I

DIFFERENCE IN TEMPERATURE (°C.) BETWEEN SURFACE SAMPLE AND WATER AT 5-METRES DEPTH AT STATION E_1.

	October.	November.	December.	January.	February.	March.
1921	+0·04°C. +0·12	−0·70° −0·04	−0·19°			
1922	+0·10	+0·01		−0·06	−0·61	−0·04
1923	+0·02	−0·18	−0·35	−0·05 −0·35	−0·11	+0·08
1924	−0·02	−0·39	−0·03	−0·06	−0·25	
1925	+0·40		−0·03	+0·01	−0·19	+0·06
1926	−0·09	−0·05	0·00 +0·08		−0·10	+0·10
1927	+0·10	+0·25	+0·12		+0·02	+0·30
1928	+0·01	0·00		+0·12	+0·17	−0·02
1929	−0·10			− ·02 − ·15	+ ·05 + ·30	0·00

FLUCTUATIONS IN THE ANNUAL CYCLE.

Not only does the maximum temperature attained at the end of summer, and the minimum temperature to which the water falls at the end of winter fluctuate from year to year, but the dates at which some particular temperature is attained differ greatly. It is perhaps the latter which is most significant to the biologist, since the breeding of many marine animals is strictly limited to a relatively narrow range of temperature. As a case in point the water near the bottom at E_1 rose to 12° C. at about the third week in June in 1921, and at the end of first week in August in 1924, and to 13° C. at about mid-July in 1921, and during the third week in September in 1924. It is obvious that such a fluctuation would have a profound effect upon any animal which breeds in the region of 12°–13° C.

The interval of about a month between each set of observations does not allow a precise value being given for the maximum and minimum temperatures attained each year by the surface water at Station E_1, but tolerably approximate values can be taken from faired curves for these temperatures and the dates they were attained in deeper water. These are shown in Table II.

TABLE II.

Approximate Maximum and Minimum Temperatures Attained by the Lower Stratum of Water at Station E_1, and Dates at which such were attained.

Year.	Maximum temperatures.	Minimum temperatures.
1921	15·4° C. third week in October	— —
1922	14·2 end September	9·5 early April
1923	13·5 first week in October	9·2 March
1924	13·1 early October	7·9 March
1925	13·6 end first week in October	9·1 late March
1926	14·5 third week in October	9·3 March
1927	13·7 early October	9·0 late March
1928	14·7 early October	8·9 early February
1929	14·0 (?) end of first week in October	8·4 early March

The isopleth diagrams in Figures 5, 6, and 7 show the temperature changes which have taken place each year at Station E_1. Black circles indicate the dates upon which series of observations were taken, and from which the isopleths are drawn.

The general distribution of temperature in the western part of the English Channel during the winter of 1927–28 is shown on the charts in Figure 8. These are compiled from surface temperatures on the cross-Channel steamship routes shown in Figure 1. They show the loss of heat during November to be most rapid in the less deep area to the eastward, which is a general phenomenon.

With regard to the fluctuations from year to year there is, I think, only one outstanding instance where the inflow of warmer water unmistakably and materially affected the cycle ; in the autumn of 1921. During other years inflow of warmer or colder water undoubtedly took place from time to time (March, 1928), but the effect of such upon the temperature cannot be clearly distinguished from the effect of fluctuating meterological conditions—solar radiation, dryness of the atmosphere leading to increased evaporation, and clear sky at night leading to increased radiation of heat into space.

In Figure 9 the observed salinities of the water at various depths at E_1 are given for the latter part of 1921, and below the integral temperature of the whole column of water from surface to bottom. An accretion of heat took place between September 15th and October 18th, a time when the water is normally losing heat. A similar curve for the following year is given below. Presumably as a result of this inflow of more saline and warmer water, a singularly warm and late autumn was experienced (Harvey, 1925).

Fig. 1.—Circles indicate positions at which surface samples are taken at regular (fortnightly) intervals. Crosses indicate positions at which research vessels work stations or take surface samples.

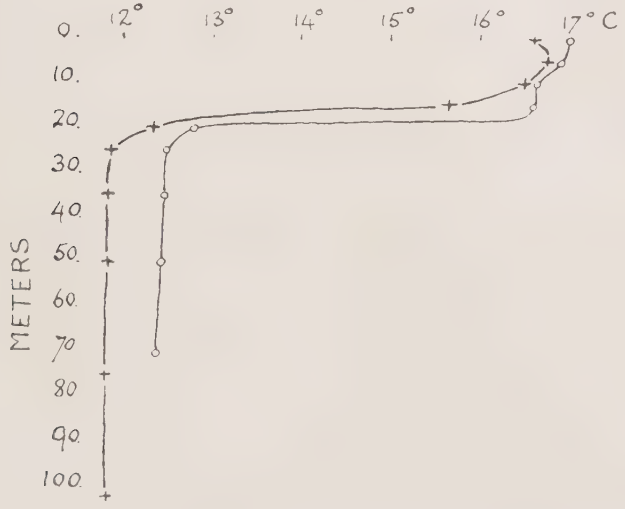


Fig. 2.—Circles indicate the temperature observed at Station E_1 on August 2nd, 1927; crosses indicate the temperature at Station E_3 on August 3rd, 1927.

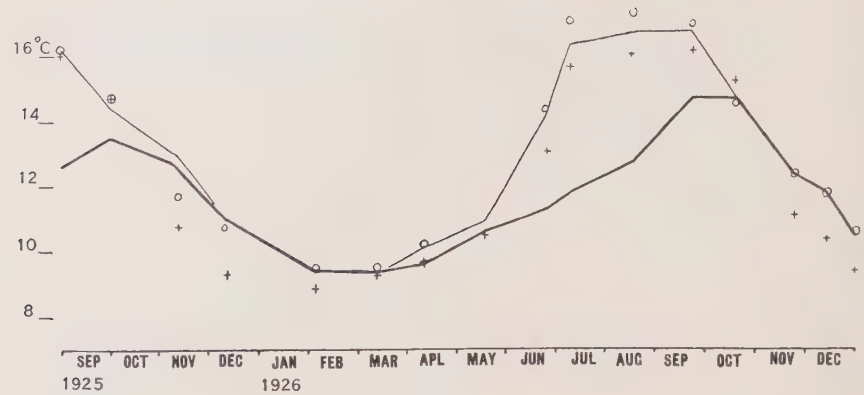


FIG. 3.—Thick line shows the temperature of the bottom water, thin line the temperature of the water at 5 metres depth, circles the surface temperatures observed at Station E_1, crosses show the surface temperatures observed off the western end of Plymouth Breakwater.

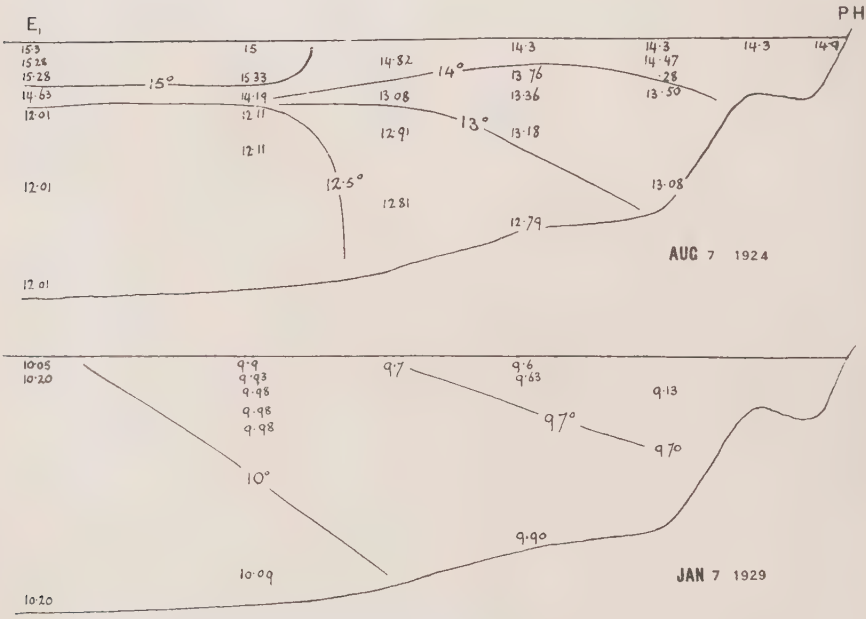


FIG. 4.—Sections between Station E_1 and Plymouth showing the distribution of temperature with depth.

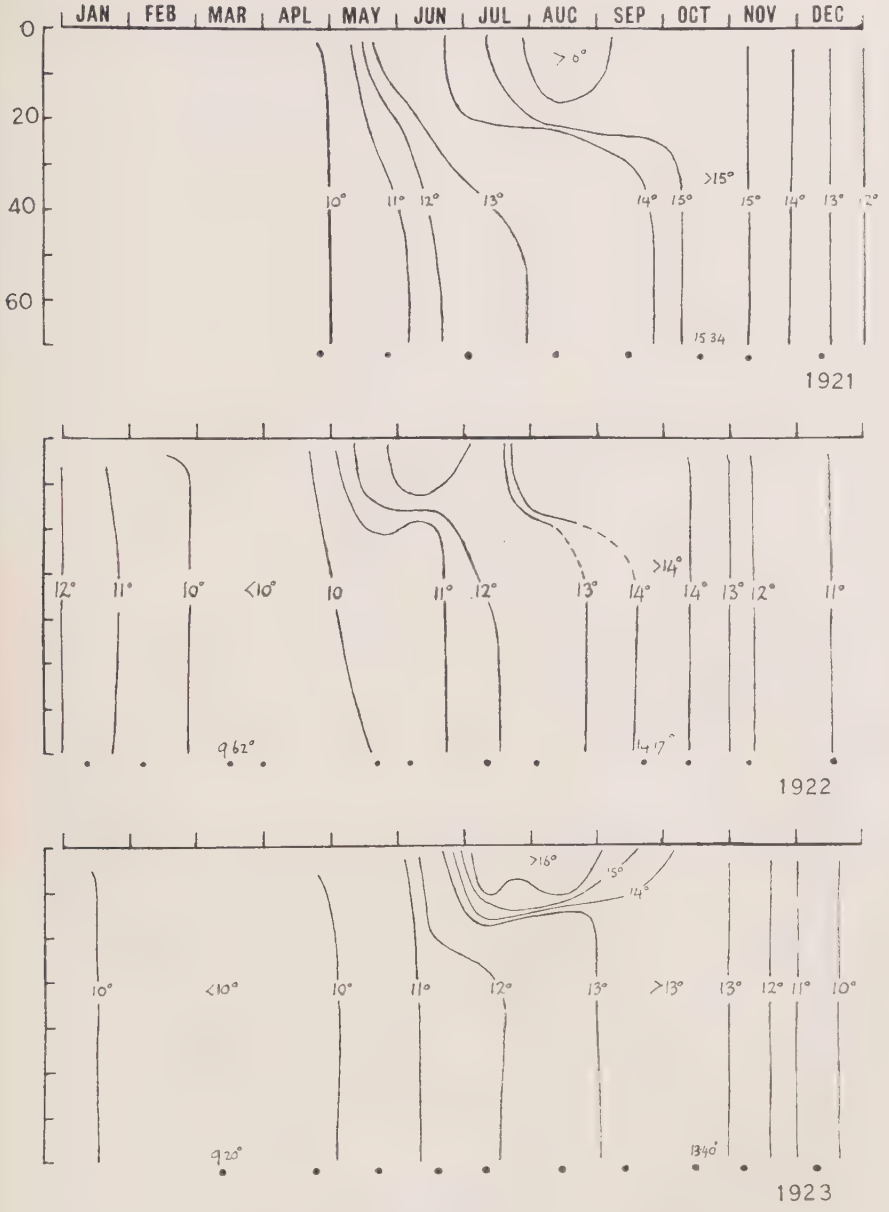


FIG. 5.—Isopleth diagrams showing the distribution of temperature with depth from April, 1921, to December, 1923, at Station E_1.

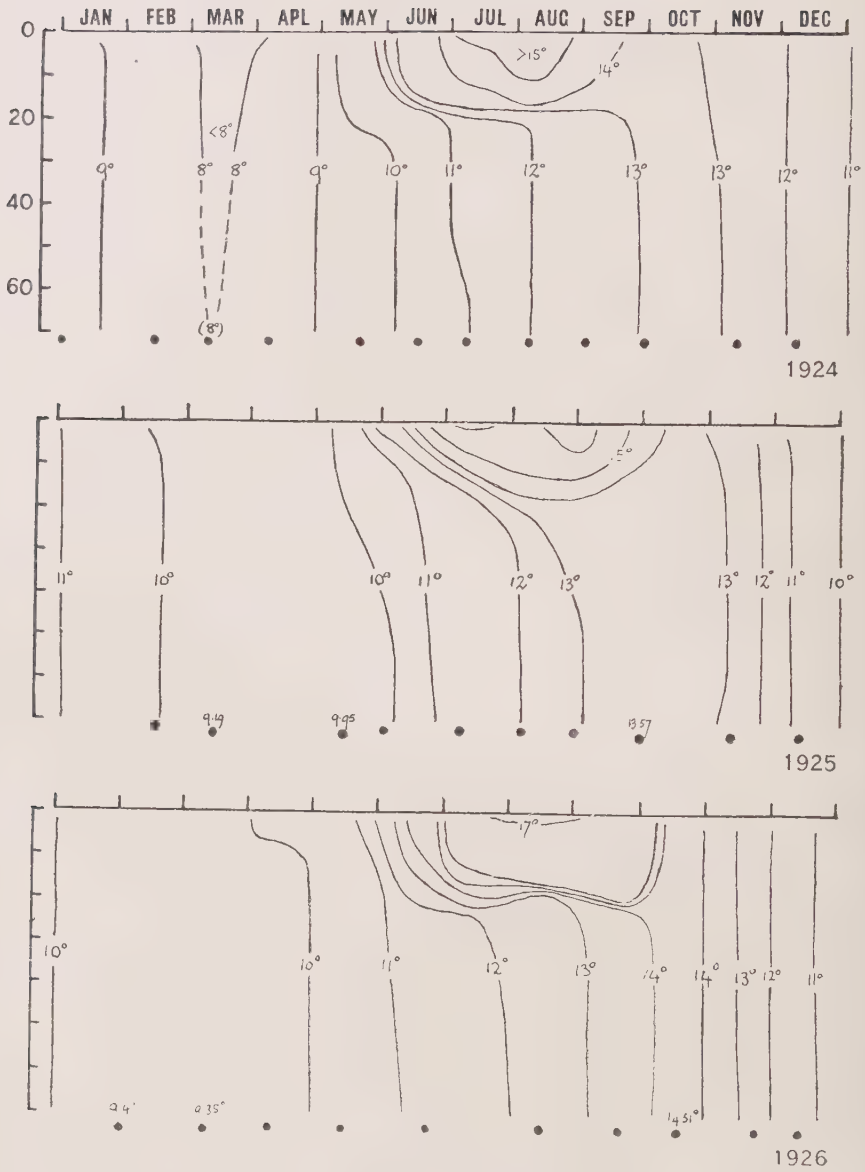


FIG. 6.—Isopleths, showing distribution of temperature with depth at Station E_1 during 1924, 1925, and 1926.

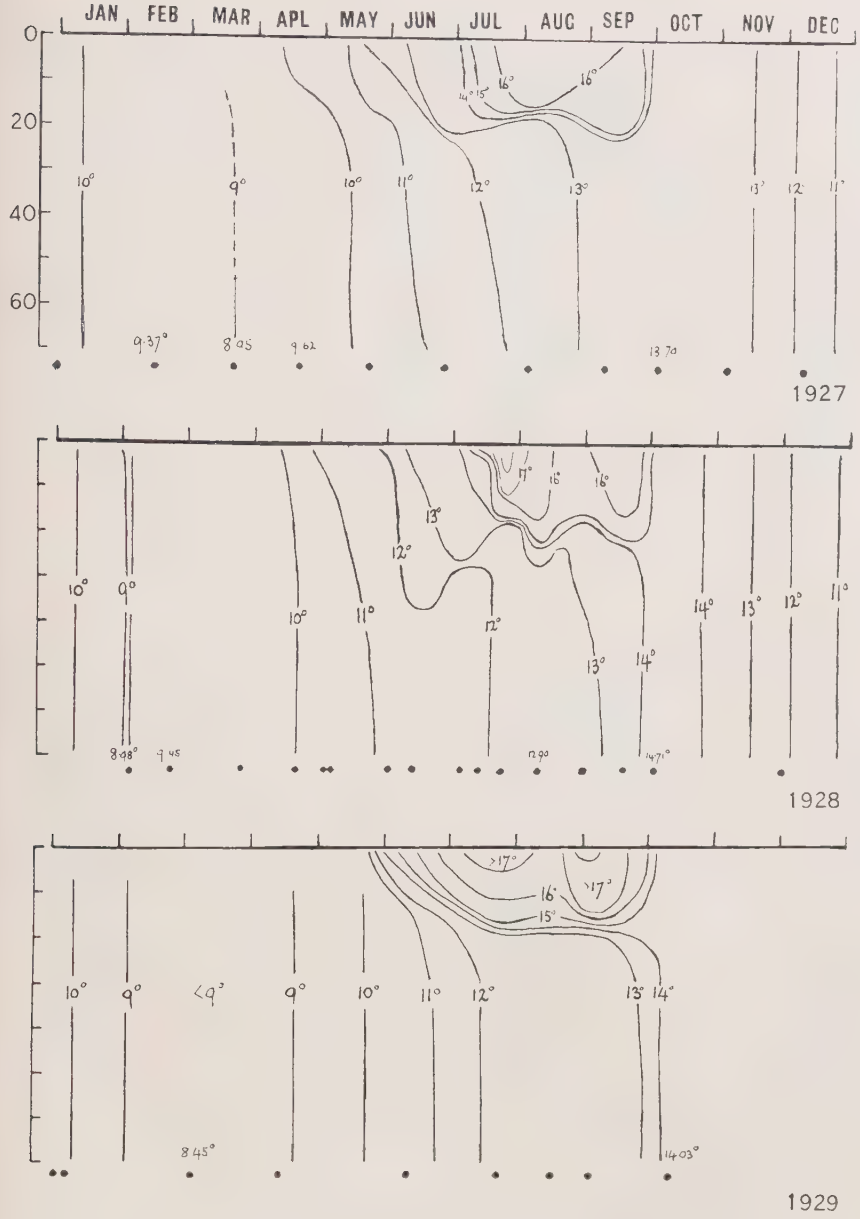


FIG. 7.—Isopleths showing the distribution of temperature with depth from January, 1927, to October, 1929.

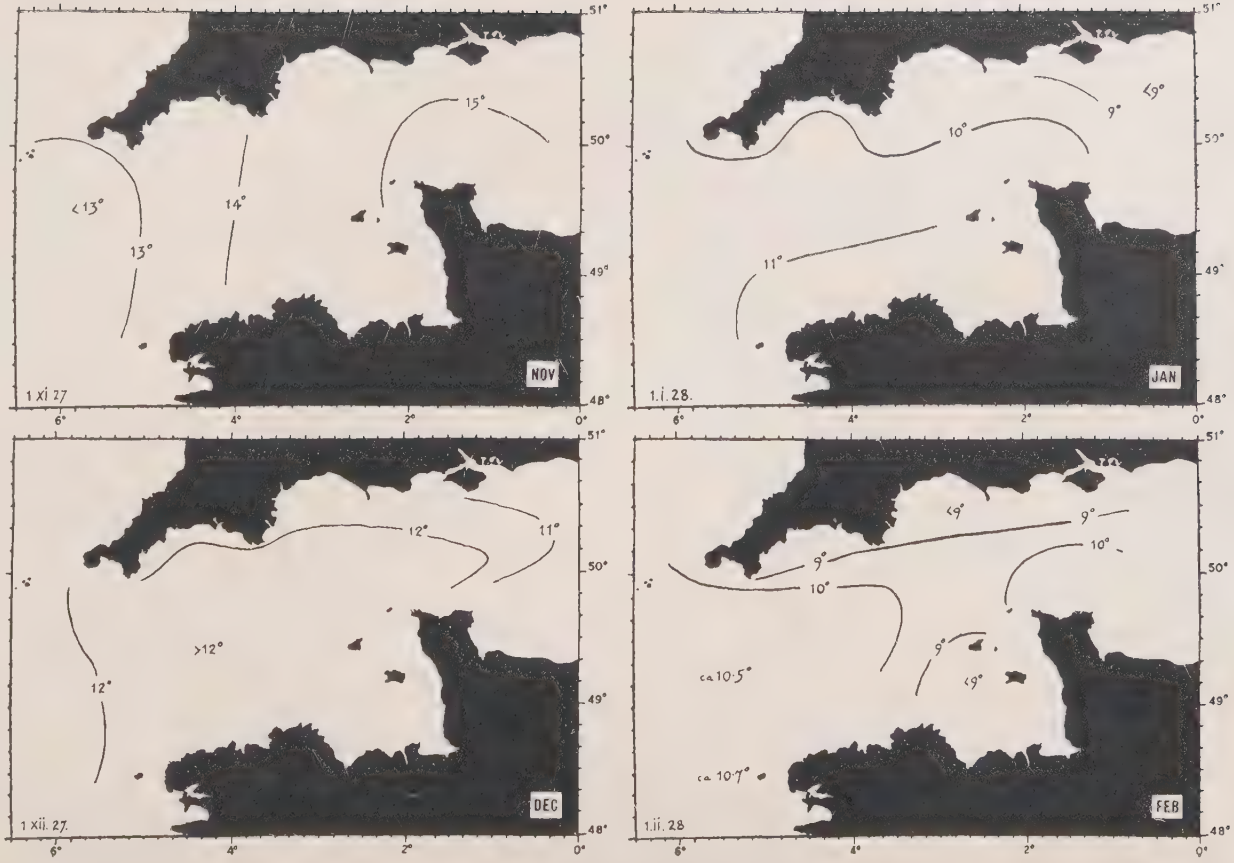


FIG. 8.—Distribution of temperature during the winter of 1927–1928.

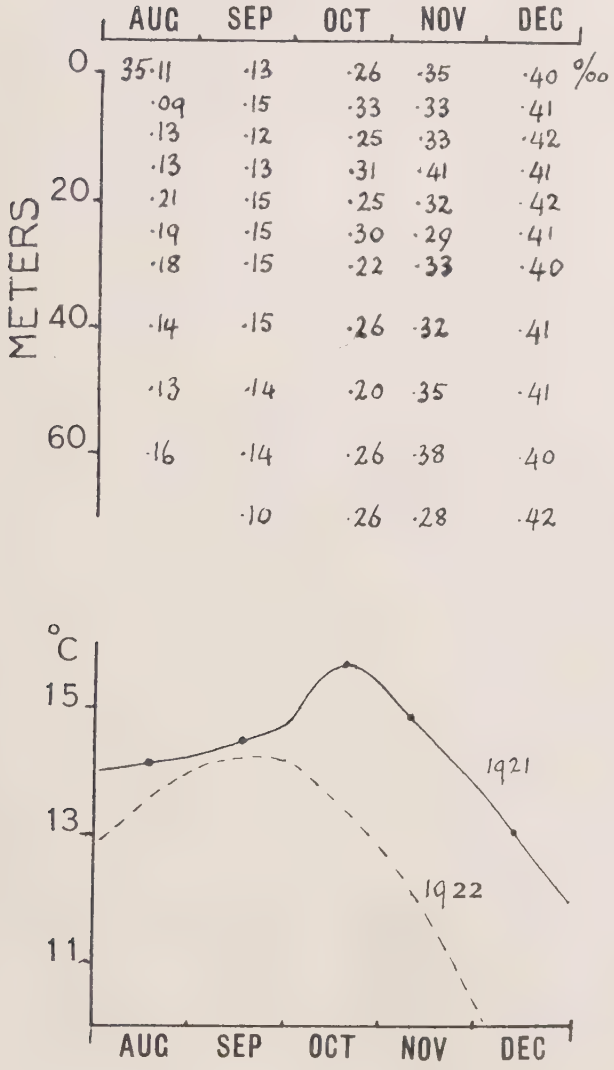


FIG. 9.—Upper diagram shows the salinity of the water observed at Station E_1 from August to December, 1921; lower diagram shows the integral mean temperature of the column of water from surface to bottom.

PART II. THE DISTRIBUTION OF SALINITY AND CIRCULATION OF THE WATER.

Our present knowledge of the circulation in the English Channel rests upon inference, with the exception of the definite proof by Carruthers (1928) that water passes through from the Atlantic into the North Sea. In this connection it is significant that the general conclusions arrived at by Matthews (1905–14) from the distribution of salinity and temperature and by Gehrke (1907) rest unaltered by subsequent observations. It does appear, however, that the circulation of the water masses, and in consequence the distribution of salinity, is more irregular and intermittent than hitherto expected.

The following brief account aims at presenting a generalised picture of the western part of the English Channel, before discussing the occurrences which are suggested by the more intense surface sampling carried out since June, 1925.

A continuous series of current measurements made by Carruthers (1928) at the Varne Light vessel shows that the residual current normally passing from the English Channel into the North Sea is occasionally held up, or even reversed for a period, by easterly and north-easterly winds, and is at other times greatly augmented by strong south-westerly winds. The mean residual movement past the Varne Light vessel at a depth of 11 metres was found to be 2·7 miles daily, into the North Sea, the maximum value so far found was 16·8 miles. The maximum residual current which occurred in the reverse direction, from the North Sea into the Channel, was 11·9 miles in a day. It was found that during the autumn months especially the flow of water into the North Sea was greatest, while during the summer months the flow was least.

Water of variable but relatively high salinity enters the mouth of the English Channel and passes eastward in the form of a tongue (Fig. 10). This tongue of water on its passage up Channel becomes more and more diluted with coastal water, itself diluted by land drainage. In spite of greater rainfall in winter, its salinity in the Straits of Dover at the Varne Light vessel is in general greater during the winter than during the summer months (Lumby, 1925, p. 14). Doubtless this is due to the increased speed of its passage up Channel and into the North Sea during the autumn and winter. A peculiar phenomenon in connection with the salinity of this tongue of water as it extends eastward has been pointed out by Lumby (1925, p. 4), who noted that during the years 1921 and 1922 the average salinity of the water increased as it passed on to the relatively shallow soundings between Newhaven and Dieppe, being higher there than where the tongue was deeper and nearer the Atlantic, on the line Southampton–St. Malo. He considered that more

saline water had crept up Channel as a subsurface current to mix with water above and so appear on reaching shallow soundings, where wave motion and tidal streaming over the bottom bring about effective vertical

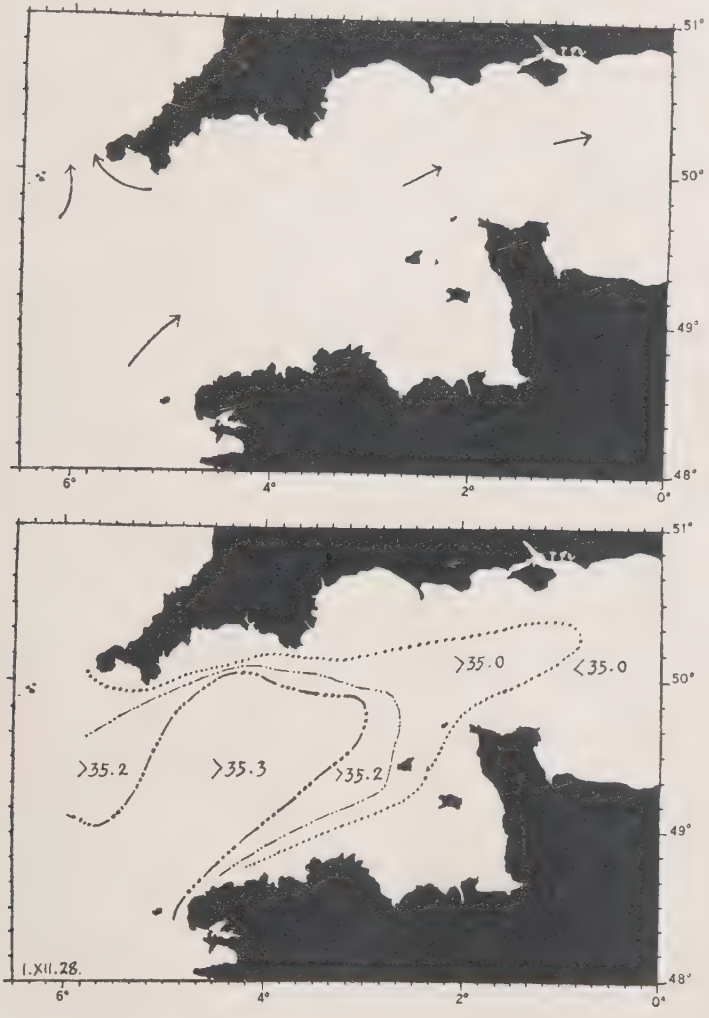


Fig. 10.—Upper diagram shows the general current system. Lower diagram shows a type of distribution of salinity expected to arise from such a system of currents.

mixing. These two years were remarkable for the inflow of highly saline water from the Atlantic. A description of the movements of bottom trailing and surface drift bottles during 1924 is given by Carruthers (1927)

who also discusses the question of cyclonic swirls set up by the penetrating tongue of water.

The shape or form of this tongue of water is very variable (Figs. 13–16). In winter the salinity is generally much the same from top to bottom ; in summer the number of cases observed where more saline water has penetrated under a layer of less saline water to any great distance are not numerous. It is considered that maps showing the surface salinity in this area are usually a fair rough picture of the salinity of the whole water mass. The picture is certainly a rough one, on account of this, of the limited intensity of sampling, and of errors likely to arise during or after rainy weather or heavy evaporation. Further, it is clear that the isohalines do not actually follow the smooth lines usually indicated in such maps, but that numerous offshoots, lacunæ and isolated patches exist.

Passing next to the circulation at the mouth of the Channel, Gehrke (1907) considered that under the centrifugal force due to the earth's rotation more water entered the English Channel than passed on into the North Sea, the surplus running out past the Lizard and Land's End. From the distribution of salinity and density, Matthews and later Lumby arrived at the same conclusion. The writer (1929) from hydrodynamical considerations found evidence that there existed a north-going difference in velocity between the surface water and the layer at 60-metres depth amounting to $1\frac{1}{2}$ miles a day between Land's End and the Scillies at the end of June, 1924.

There can be little doubt of the existence of such a residual current, superimposed on the tidal streaming, carrying water northward into the mouth of the Bristol Channel—variable in velocity and perhaps intermittent. Such a current system as suggested would be expected to give rise to a salinity distribution of the type shown in Figure 10. Changes in the current system would lead to changes in the salinity distribution ; hence the value of mapping the latter at short intervals of time in order to gauge the changes taking place in the general circulation. Such changes frequently appear to be swift and of short duration.

With regard to this general current system at the mouth of the English Channel, Matthews (1911 and 1914) found evidence of a cyclonic circulation in the southern part of the Irish Sea. Water moving northwards past Land's End and curling towards the south-east coast of Ireland moved southwards and westward to rejoin the north-going stream past Land's End. There was evidence that a similar movement of the upper layers over the stratum at 60 metres existed at the end of June, 1924 (Harvey, 1929). Matthews found evidence that the southern boundary of this cyclonic system lay further southward during the winter months. The more saline Atlantic water entering the Channel then lay closer to

Ushant, the northern part of the mouth of the Channel being blocked by the less saline water of this cyclonic system.

The water, lying at the mouth of the English Channel and forming the base of the tongue which extends eastward, is of very variable salinity. Thus in February, 1903, water of 35·5°/$_{oo}$ lay north of Ushant and in July of 1928 the whole mouth of the Channel was filled with water of under 35·0°/$_{oo}$.

As the Atlantic Stream creeps gradually northward along the edge of the continental shelf it undergoes gradual dilution : when the stream is least torpid, water of high salinity may be expected to swing from the ocean into the mouth of the English Channel under the influence of the earth's rotation. When, in addition, wind favours its passage onward and through the Straits of Dover the highest salinity at the entrance of the Channel might be expected.

These surges of the Atlantic Stream are very variable as judged by the change in latitude of the isohalines in the open ocean and the salinity of the water which penetrates, perhaps welling up, into the relatively shallow soundings at the mouth of the English Channel and in the Irish Sea.

The most notable effects recorded are those in 1903 when high salinity water persisted for over two years and again in 1921. In the early summers of 1923 and 1928 an unusual condition was observed. After heavy rains in the Loire watershed (Atkins, 1929) the English Channel filled with water of abnormally low salinity, much of which apparently came from the west coast of France, moving northward and entering the Channel past Ushant. By July, 1928, the entire Channel was filled with water having a salinity of less than 35·0°/$_{oo}$ (Figs. 15 and 16).

The Surface Salinity Diagrams.

The routes along which samples have been taken, about twice monthly, are shown in Figure 1, in which circles indicate the usual positions of sampling. The data obtained since June, 1925, when the line Plymouth–Guernsey was commenced, have been plotted in the manner shown in Figure 11. It is usually simple to draw lines marking salinities of 35·0, 35·2, 35·3, etc., and so obtain moderately true isopleths indicating the change in salinity with time and with position along the particular route. Not infrequently high salinities are found at one or two positions at a particular date, while no such high values were obtained either a fortnight previously or a fortnight later. This may mean that a narrow tongue has penetrated to the position shown and breaks up to disappear by mixing with the surrounding water mass during the ensuing fortnight, or alternatively that an outlying patch happened to be passing across the

route. In some instances further evidence can be obtained from stations in the neighbourhood which have been sampled at various depths within a few days of the occurrence by a research vessel.

From these isopleth diagrams 43 charts have been prepared showing the distribution of surface salinity at the beginning of each month. Lines are drawn connecting up the positions at which salinities of 35·0, 35·2, 35·3, etc., occur on each route, wherever possible due regard being paid to data obtained shortly before or after at various depths by the research vessels.

There can be little doubt that these boundary lines are in fact very

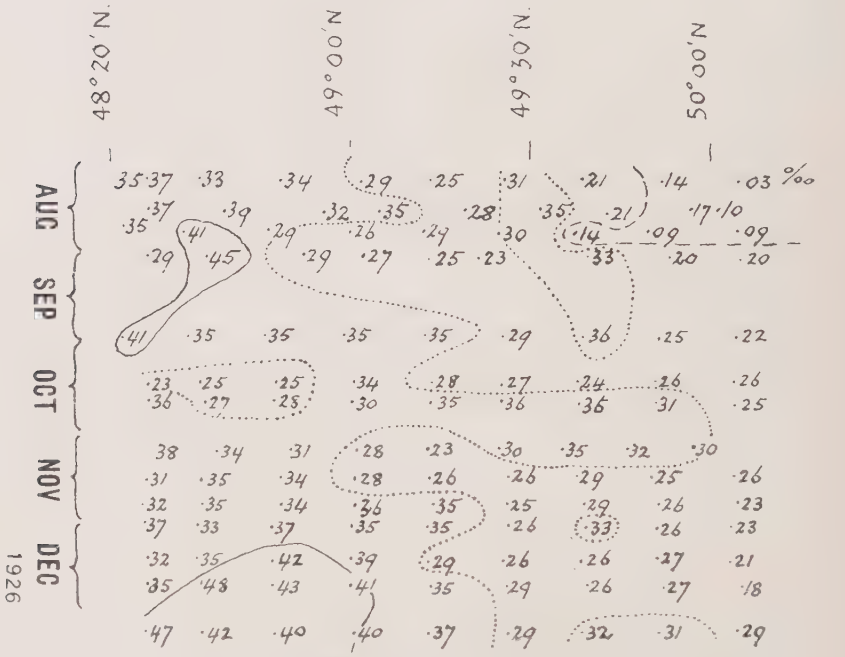


Fig. 11.—Portion of surface salinity isopleth diagram across the mouth of the English Channel (line Longships L.V. to Ushant).

irregular, with indentations, lacunæ, and outlying patches, but the fair lines drawn in such diagrams are the only means of indicating the general distribution without having data from impracticably intense sampling. Further, on some occasions less saline water lies over more highly saline or *vice versa*, the isohalines lying obliquely, not vertically; an outlying patch may be near the surface and not extend to the bottom, as was found by Matthews on occasions.

However, on taking the available evidence as a whole, a conclusion does seem justifiable that such charts give a tolerable rough picture of the

distribution of the water masses on most occasions. Any inferences regarding the movements of the water masses, as deduced from the changes they bring about in the distribution of surface salinity, rest upon the validity of the above conclusion. In the area under discussion there have been only a limited number of stations worked from top to bottom within two or three days of each other since June, 1925. If we consider a wide area, however, the distribution in February, 1927, is interesting because the French, Irish and our own vessels worked lines of stations all between the 15th and 18th. In Figure 12 the surface salinities along the steamship routes marked with circles are filled in from isopleths, and the actual observed salinities along the routes followed by the research vessels are for the most part shown in the sections. In the deep water south of Ireland the isohalines are not usually vertical—the presence of layers of more saline water sandwiched between less saline water above and below was particularly noticeable during the summer of 1929. Towards the eastern end of the English Channel and in the shallower part of the North Sea the salinity is usually the same from top to bottom. In such areas, therefore, changes in the distribution of surface salinity are more nearly representative of the movements of the water masses.

Turning next to the 43 distribution diagrams from June, 1925, to December, 1928, we find during this time an irregular inflow of high salinity water from the Atlantic into the mouth of the Channel and its disappearance. The most marked and lasting instances are shown in Figures 13, 14 and 16 respectively, while in Figure 15 is shown an incursion of low salinity water rounding Ushant and passing into the English Channel.

From June, 1925, to the end of 1926 water having a salinity of over 35·3°/$_{oo}$ usually lay to the westward of the line Lizard Ushant. However, during the month of January, 1926, there was a marked incursion of this water into the Channel extending to about 2° 40′ W. long. (Fig. 13). By the beginning of March it appeared to have mostly moved north-westward and on April 1st was only found in the neighbourhood of the Scillies. During the next three months there was a fall in salinity in the mouth of the Channel and at the beginning of July the mouth was filled with water having a salinity less than 35·2°/$_{oo}$. It is not clear how this fall in salinity arose. There is no reason to suppose that on the whole low salinity water from the North Sea moved into the Channel during the period February to June, nor is there any decided indication of low salinity inshore water from the west coast of France entering the English Channel through the Le Four Channel or close to Ushant.

If we consider the distribution of the water masses having a salinity greater than 35·3°/$_{oo}$ on February 1st, 1926 (Fig. 13), it is difficult to conceive how this great mass of water can have become diluted by

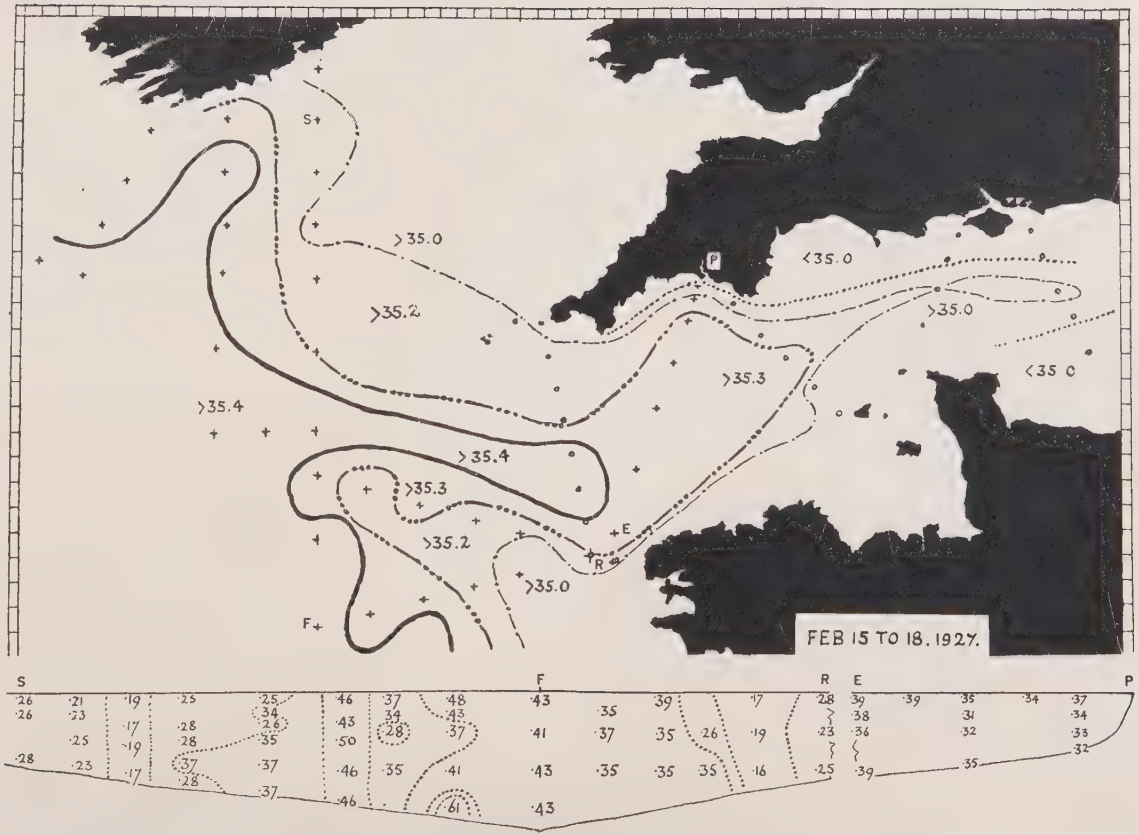


FIG. 12.—Chart showing the distribution of surface salinity, February 15th to February 18th, 1927. Sections P to E, R to F, F to S, showing the distribution of salinity with depth between the same dates.

infiltration and mixing along the edges within two months to give rise to the condition shown for April 1st. It seems much more probable that most of it had slowly swirled away north-westward, retaining its characteristic salinity, and had been largely replaced. The same argument applies even more clearly to the changes portrayed during March, April, May, and June, 1927, in Figure 14. Even in the case of a small patch or outlier of water, having a salinity greater than that of the surrounding water mass, and a surface area of no more than one or two hundred square miles, it is difficult to conceive that it would mix horizontally with the surrounding less saline water at all rapidly. Rather it might be expected that much of it would retain its characteristic higher salinity for several weeks or more.

From July, 1926, to December no samples were obtained on the Plymouth–Guernsey route, and the other data do not show any remarkable changes.

From December, 1926, to March, 1927, a decided inflow of Atlantic water into the mouth of the Channel is shown in Figure 14. The inflow indicated as taking place during December represents a volume of water of over 120 cubic miles. Current measurements at the Varne Light vessel indicate that during this month of December about 18 cubic miles of water per day passed from the North Sea into the English Channel—a reversal of the usual direction of the residual drift. Hence, in order to make way for the incoming Atlantic water, it is not improbable that over 120 cubic miles of water passed out of the Channel round the Lizard and Land's End. Assuming that this west-going stream extends for about 12 miles off shore, its velocity residual to the to and fro tidal streaming would average about 9 miles per day, perhaps rather more, during this particular month. Tidal stream observations off the Lizard in calm weather, probably only in summer, indicate a residual component in a westerly direction. " Off the Lizard the streams are of nearly equal duration, the west-going stream running . . . at a maximum rate of 3 knots near the rocks ; and the east-going stream . . . at a maximum rate of 2 knots at springs " (*The Tides and Tidal Streams of the British Isles*, Tizard, p. 43, 1909). During March, 1927, the $35{\cdot}3^{\circ}/_{\circ\circ}$ salinity water penetrated far into the Channel in the form of a narrow tongue (Fig. 14) ; some 35 cubic miles of water passed during the month into the North Sea helping to draw this tongue westward. During April, May, and June this formation broke up and there is indicated a gradual retreat north-westward of the higher salinity water.

From July, 1927, to March, 1928, there were no considerable intrusions of high salinity water.

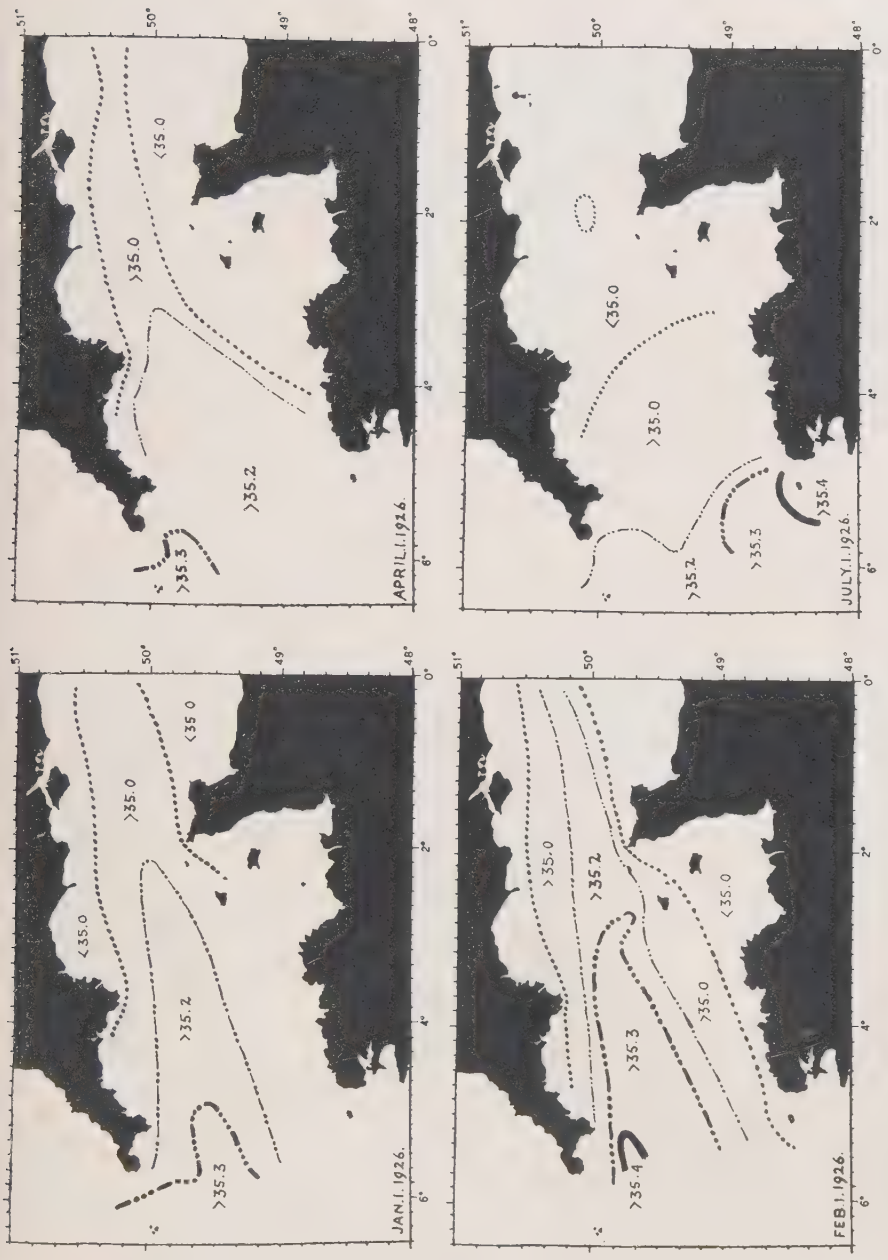
During March and April, 1928, the mouth of the Channel filled up with low salinity water (Fig. 15), unusually transparent and rather warmer

than usual for the time of year. It is suggested (Atkins, 1929) that this water came in part northward from the west coast of France, rounding Ushant into the English Channel, and in part from drainage from the Seine watershed. In the Loire and Seine basins the rainfall during February was approximately 75% above normal, and 50 to 60% above normal for the three months January, February and March. This low salinity water possibly overlay water of higher salinity in the neighbourhood of Ushant, at all events such a condition was found later on May 8th (Fig. 15, section).

Such a condition was only observed once before since 1921, when an upper layer of water having a salinity less than 35·0‰ was found extending some 60 miles north of Ushant in April, 1923. During this year also the rainfall in the Loire and Seine basins was exceptionally high, approximately 100% above normal for the month of February.

The next change of considerable extent is the inflow of higher salinity water commencing in July, 1928, and culminating on or after December, 1928 (Fig. 16).

The proofs of this paper have been read by Lieut.-Comdr. J. R. Lumby, to whom I am further indebted for several suggestions.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>35.3
>35.4
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>35.0
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<35.0
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51°
50°
49°
48°
6°
4°
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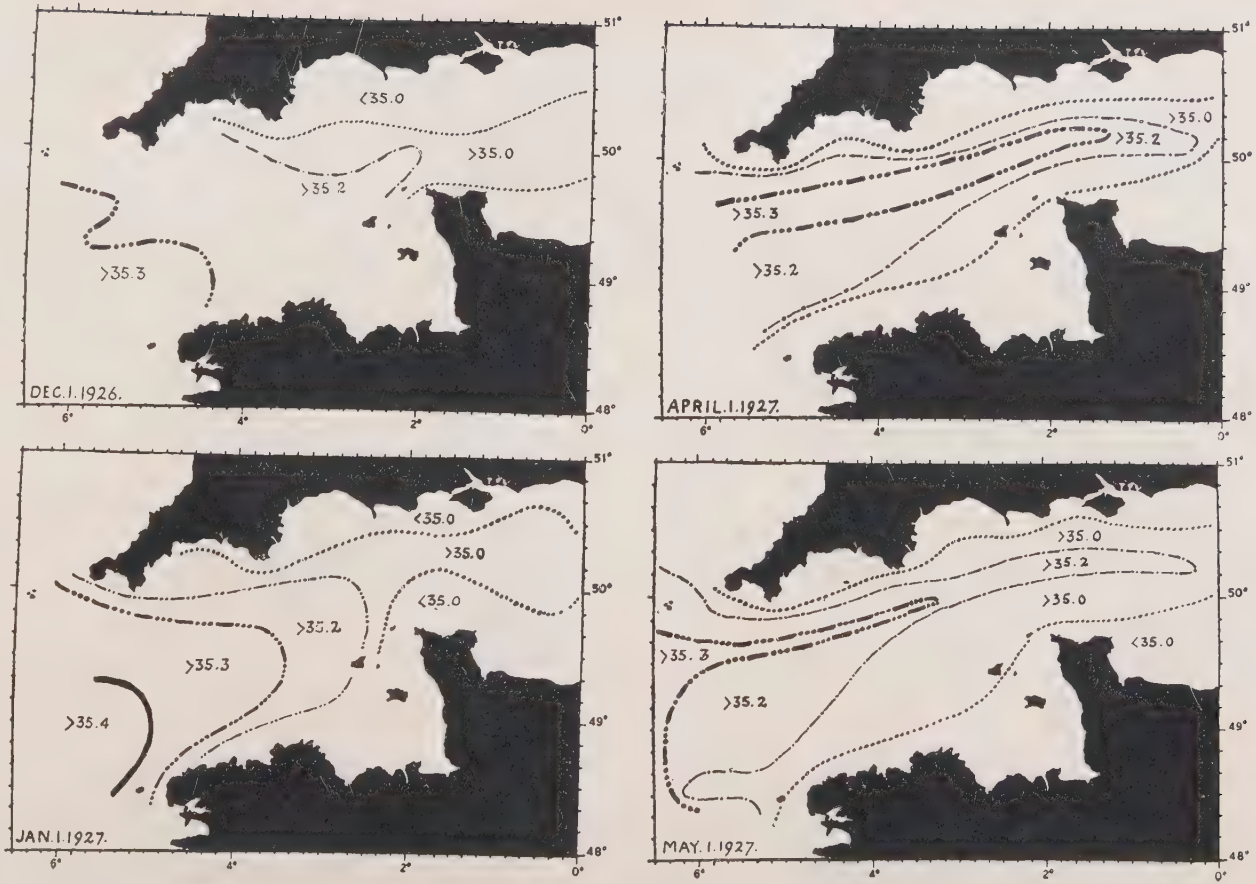
0°

FIG. 13.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JAN. 1. 1927.
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>35.2
>35.0
>35.3
<35.0
>35.2
MAY. 1. 1927.
51°
50°
49°
48°
6°
4°
2°
0°

FIG. 14.

FIG. 14 (*continued*).

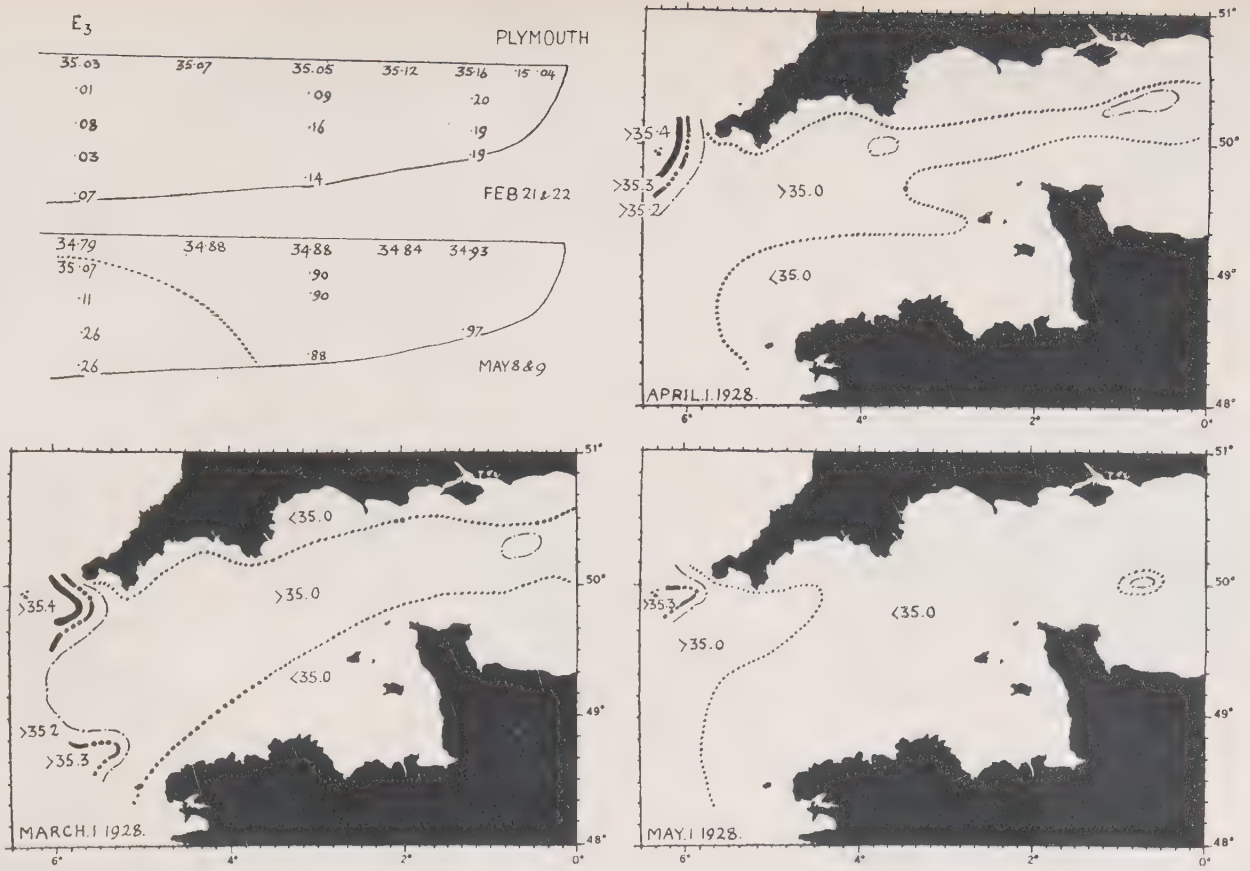
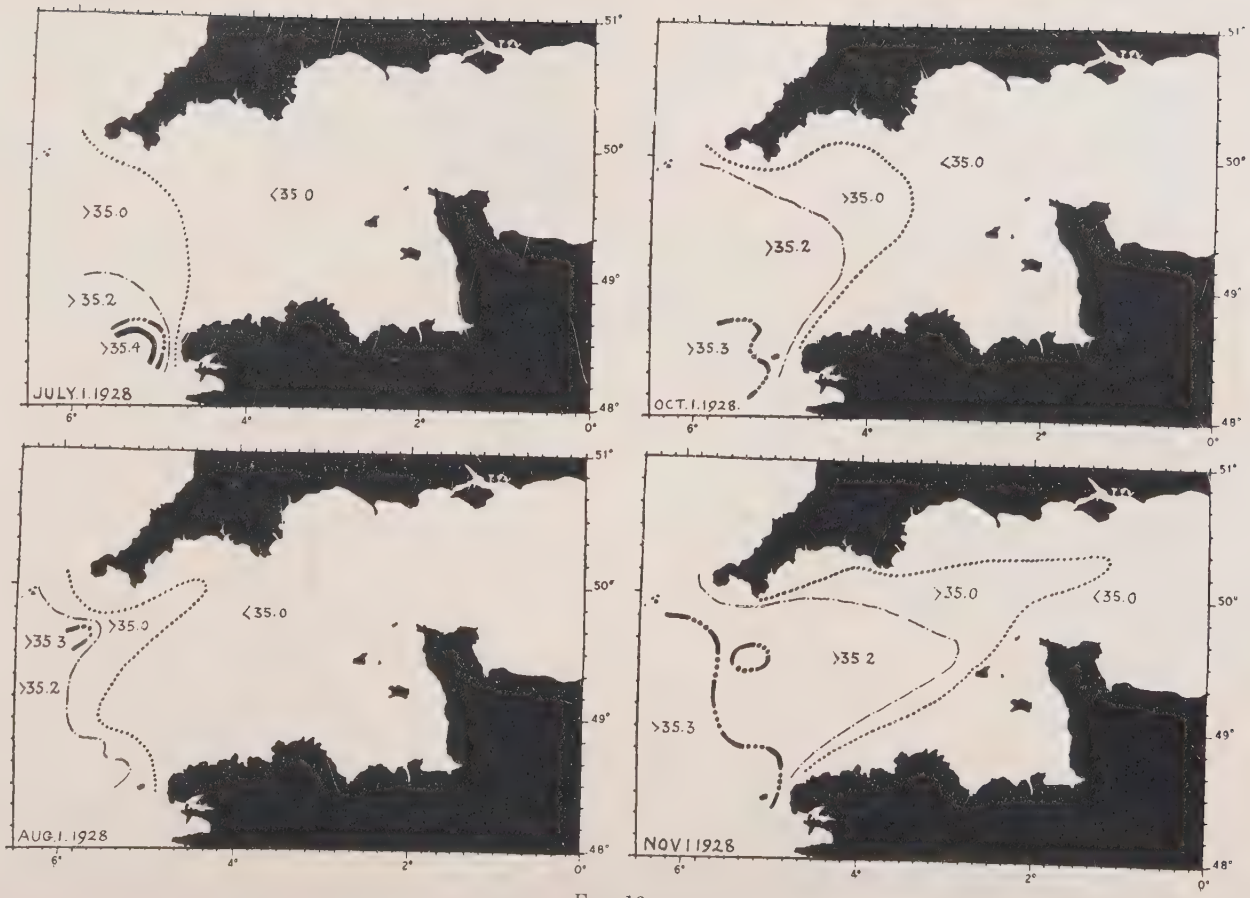

E3
PLYMOUTH
35·03 35·07 35·05 35·12 35·16 ·15 ·04
·01 ·09 ·20
·08 ·16 ·19
·03 ·19
·07 ·14
FEB 21 & 22
34·79 34·88 34·88 34 84 34·93
35·07 ·90
·11 ·90
·26 ·97
·26 ·88
MAY 8 & 9
APRIL 1. 1928.
MARCH 1 1928.
MAY 1 1928.
>35·4
>35·3
>35·2
>35.0
<35.0
51°
50°
49°
48°
6°
4°
2°
0°

Fig. 15.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OCT. 1. 1928.
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>35.0
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AUG. 1. 1928
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>35.0
>35 3
>35.2
NOV 1 1928
>35.0
<35.0
>35 2
>35.3
51°
50°
49°
48°
6°
4°
2°
0°

FIG. 16.

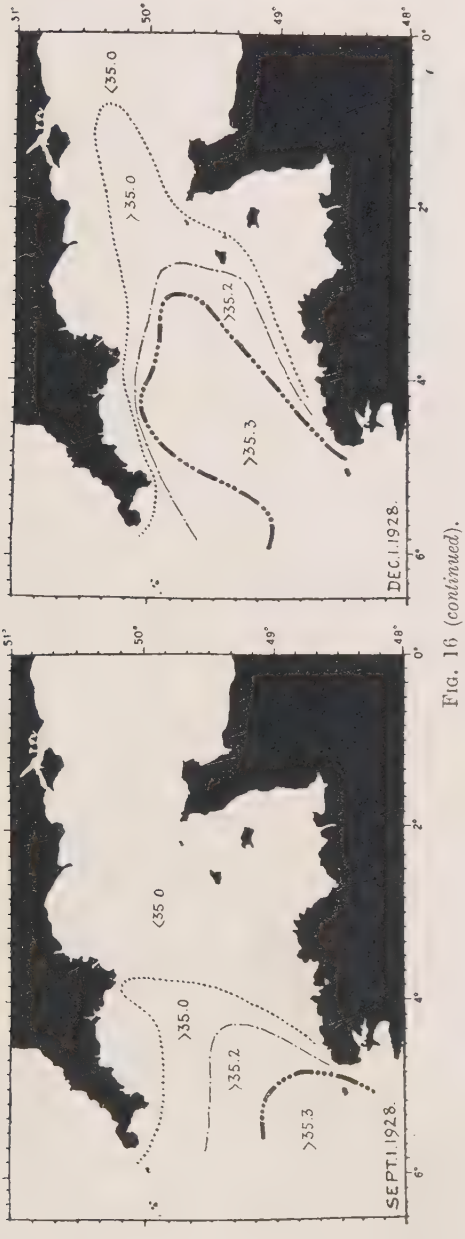

Fig. 16 (*continued*).

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Seasonal Variations in the Phosphate and Silicate Content of Sea-Water in Relation to the Phytoplankton Crop. Part V. November 1927 to April 1929, Compared with Earlier Years from 1923.

By

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Head of the Department of General Physiology at the Plymouth Laboratory.

With 12 Figures in the Text.

Introduction.

In the previous numbers of this series (1923, 1925, 1926, 1928) it was fully established that the phosphate and silicate content of sea-water becomes greatly reduced in spring and summer. It is possible to calculate a minimum value for the phytoplankton crop from the amount of phosphate used up, also to ascertain the production up to and between various dates; such information has a direct bearing on the supply of food for copepods and other animals upon which young fish feed. The accumulation of data of this type should in time permit of some generalization as to the favourableness or otherwise of any season with respect to the survival of relatively large numbers of young fish of various species in the locality studied. The present paper is a further contribution towards the amassing of seasonal productivity data which has been in progress since March 1923, with a gap from March to October, inclusive, during 1927. Information has moreover been sought as to the extent to which the removal of the phosphate approaches completion; the analyses of water samples low in phosphate have been carried out with a rather greater degree of accuracy than heretofore, by using a more exact method of allowing for the reagent blank, by using weaker standard solutions and by ensuring that in nearly every case the analyses were performed on the day following that on which the water samples had been taken. When the cruise extended for two days this was not possible as regards samples taken on the first day. Furthermore, measurements have been made (Poole and Atkins, 1928) of the illumination, both aerial and submarine, obtaining when the samples were taken.

Seasonal Variation in Phosphate Concentration of Water at International Hydrographic Station E1.

The data from November 1927 to April 1929 are shown in Table 1, also records of silica content, temperature, vertical illumination, in air and at 10 and 20 m., together with the percentages of the illumination penetrating to these depths. The variation of phosphate with depth is shown in Figure 1, in which data from an earlier paper, but not previously plotted, have been incorporated. The phosphate-depth lines move to the left as the year goes on and concentration decreases. Then follows a period when the water may be almost or quite devoid of phosphate down to 20 m., while simultaneously regeneration preponderates in the deeper water. A little later active regeneration takes place at the surface,

TABLE 1.

STATION E1. The first line shows the dates on which samples were taken and top portion of the table gives phosphate results as mg. P_2O_5 per m.^{3}, A denoting date surface and bottom. Below these are temperatures. In the lowermost section, opposite V, electrically in air. Immediately below are the percentages of the illuminations reaching refer to measurements made about midday, the values opposite V, from which they are

	1927		1928											
M	4/11	9/12	31/1	21/2	1/3	27/3	5/4	19/4	2/5	7/5	8/5	4/6	13/6	4/7
0	19†	31	43‡	27	33	28	24	24	10	9	9	9	4	12
5	20	—	35	27	26	25	25	23	10	9	—	9	3·5	4·5
10	—	—	36	—	28	—	—	—	—	10	—	—	5	4·5
15	—	—	—	—	—	25	—	—	10	22	—	—	—	3·5
20	—	—	—	—	—	—	—	—	17	18	—	9	5	—
25	—	—	—	—	—	26	—	—	18	18	—	—	—	4
30	—	—	—	—	—	—	—	—	—	19	—	10	—	15
35	—	—	—	—	—	—	—	—	—	—	—	9	7	—
40	—	—	—	—	—	—	—	—	—	—	—	—	10	18
50	—	—	—	—	—	—	26	—	—	—	—	—	14	19
70	25	31	36	28	29	41	27	23	20	19	20	13	14	25
A	8/11	12/12	1/2	27/2	2/3	29/3	7/4	20/4	3/5	9/5	11/5	6/6	14/6	6/7
0	313	260	260	220	220	170	130	78	92	—	—	—	59	33
70	326	300	260	210	210	176	130	78	78	—	—	78	78	78
A	7/11	10/12	1/2	28/2	2/3	30/3	10/4	20/4	3/5	—	—	6/6	18/6	6/7
0	13·4	12·1	9·1	9·7	9·7	9·6	9·8	10·1	11·4	12·5	12·4	12·1	13·1	14·1
5	13·5	11·9	9·0	9·5	9·5	9·6	9·8	10·1	11·3	12·2	—	11·9	13·1	13·9
10	„	„	„	„	9·3	„	„	„	11·1	10·9	—	—	12·7	13·6
15	„	„	„	„	„	„	„	10·0	10·5	10·3	—	11·9	—	13·4
20	„	„	„	„	„	„	„	„	10·3	10·3	—	11·9	12·4	13·4
25	„	„	„	„	9·3	„	9·7	„	„	„	—	11·9	—	13·2
30	„	„	„	„	„	„	—	10·0	10·2	10·2	—	11·9	12·3	11·8
40	„	„	„	„	„	„	—	„	„	„	—	11·5	11·8	11·7
70	13·5	11·9	9·0	9·5	9·2	9·6	—	10·0	10·2	10·2	10·2	11·1	11·2	11·7
V	—	30·8	—	—	66·5	66·5	86	134	—	86·5	—	—	48·5	126
10	—	23%	—	—	24%	15%	21%	35%	—	32%	—	—	30%	18%
20	—	8%	—	—	9%	5%	6%	16%	—	14%	—	—	11%	4%
10		7·1			16·0	10·0	18·1	47·0		27·7			14·5	22·7
20		2·5			6·0	3·3	5·2	21·4		12·1			5·3	5·0

† At L4, 20 mg. surface and 22mg. bottom. ‡ At L4, 92 mg. surface and 32 mg. bottom.

as on September 22nd and October 19th, 1926, also August 16th and 29th, 1928. The vertical mixing of the water, which occurs late in September or early in October, may be followed by a diatom outburst, as shown by the decrease in the mean phosphate concentration of the column. Mixing is usually rapid throughout the isothermal column which obtains in winter, but at times regeneration may be sufficiently rapid at the surface to give markedly greater values, as on November 24th, 1926, March 21st, 1927, and January 2nd, 1929. This appears to be due to the decomposition of organic matter floating up to the surface.

In Figure 2 the phosphate data for 5 m. and bottom, 70 m.—the depth of water is about 70–73 m. actually—are shown throughout the same years. In order to avoid the irregularities introduced by surface regeneration in hot summer weather, when according to Marshall and Orr (1928)

TABLE 1 (*contd.*)

observations made from 1927–1929. The first column records depths in metres. The on which analyses were performed. The next portion shows silicate as mg. SiO_2 per m.^{3}, are shown the vertical illuminations in thousands of metre candles, as measured photo- 10 and 20 m. At the bottom the actual illuminations at these depths are given; they calculated, being the maxima observed for the day.

	1928								1929				
M	11/7	23/7	9/8	16/8	29/8	18/9	2/10	30/11	2/1	7/1	4/3	26/3	11/4
0	8·5	0	0·5	34	24	5	11	26·5	48	40	31·5	4	13·5
5	1·5	0	0	1	3·5	5	12·5	27	33·5	37	31·5	29	11·5
10	2	1·5	0	0	9	—	—	—	—	—	—	30	11·5
15	2	1·5	0·5	6	10	5·5	—	—	—	—	—	—	12·5
20	4	10·5	1	5·5	15	10	—	—	—	—	—	—	12·5
25	8·5	15	10	17	—	25	13	—	—	—	—	31	14
30	20	13	13	17·5	15	25	—	—	—	—	—	—	14
35	–	–	—	—	—		—				–	—	—
40	19	13	—	—	—	—	—	—	—	—	—	—	14
50	—	14	12	12·5	19			—				34·5	—
70	24	14	19	13	19	25	13	29	33·5	35·5	31·5	36	17·5
A	12/7	24/7	11/8	18/8	30/8	19/9	4/10	1/12	4/1	9/1	6/3	28/3	12/4
0	33	59	98	—	120	98	163	196	183	—	220	—	—
70	78	137	130		130	210	163	196	183		228	—	—
A	12/7	25/7	11/8	—	31/8	20/9	4/10	3/12	4/1	—	6/3	—	—
0	16·1	18·2	16·6	16·0	15·9	16·8	14·9	12·1	10·5	10·0	8·5	9·2	8·8
5	14·8	18·1	16·5	15·8	15·7	16·6	14·7	12·1	10·7	10·2	8·5	8·7	8·8
10	14·1	17·4	16·4	15·8	15·7	16·5	14·7	—	—	—	—	8·7	8·8
15	13·7	15·1	16·3	15·7	15·1	16·3	14·7	—	10·7	—	—	8·7	—
20	13·2	12·7	15·9	14·9	13·6	15·5	—	—	—		—	—	—
25	12·3	12·6	13·4	12·7	13·6	13·8	14·7	12·1	—		—	—	—
30	11·8	12·6	13·0	12·7	13·4	13·7	–	—	—	–	—	—	—
40	11·8	12·5*	12·9	12·7	12·9	13·5	14·7	—	10·7	—	—	—	—
70	11·8	12·9*	12·9	12·9	12·7	13·5	14·7	12·1	10·7	10·2	8·5	8·6	8·8
V	130	120	56	—	111	78	65	15·3	15	—	—	—	—
10	25%	47%	16%	—	24%	36%	16%	18%	24%	—	—	—	--
20	6%	16%	2%	—	8%	16%	4%	5%	9%	—	—	—	-
10	32·5	56·4	9·0		26·7	28·1	10·4	2·7	3·6	—	—	--	—
20	7·8	19·2	1·1		8·9	12·5	2·6	0·8	1·4	—	—	–	--

* Confirmed by duplicate observations.

the light near the surface is far too bright for effective photosynthesis by diatoms, the 5 m. values have been plotted. In July and August the surface concentrations may reach zero. The "zero" concentration really means less than 0·5 mg. P_2O_5 per m^3., or quite certainly less than 1 mg. when compared most carefully with reagent blanks. Presumably

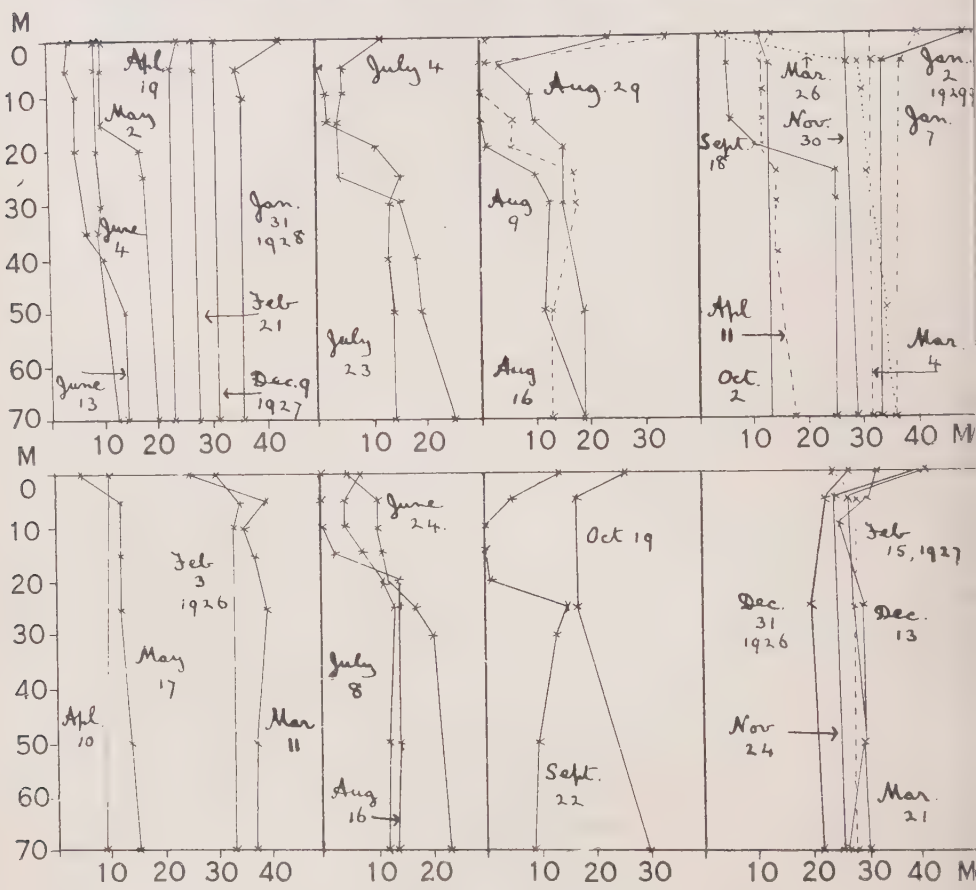

FIG. 1. Variation of phosphate concentration with depth at Station E1. The lower portion concerns 1926 up to February 1927; the upper portion concerns December 1927 to April 1929. For the sake of clearness the curves for the months have been plotted in four panels, in both upper and lower portions. Phosphate is shown as mg. P_2O_5 per m^3. From data of Table 3 (Atkins, 1928) and Table 1, this paper.

it is on account of their minute size that the diatoms are so effective in removing phosphate.

The chief interest in Figure 2 lies, however, in the evidence it affords as to the date of the main spring outburst of phytoplankton, which, it may be seen, occurs much later in some years than in others. The

magnitude of the crop depends upon the change in the water as a whole ; this will be considered later.

While the upper water is almost devoid of phosphate, regeneration proceeds apace in the bottom water, as shown by the peaks in the lower curve. The phosphate thus set free is gradually brought up into regions of better illumination and is used up by the phytoplankton, so that it

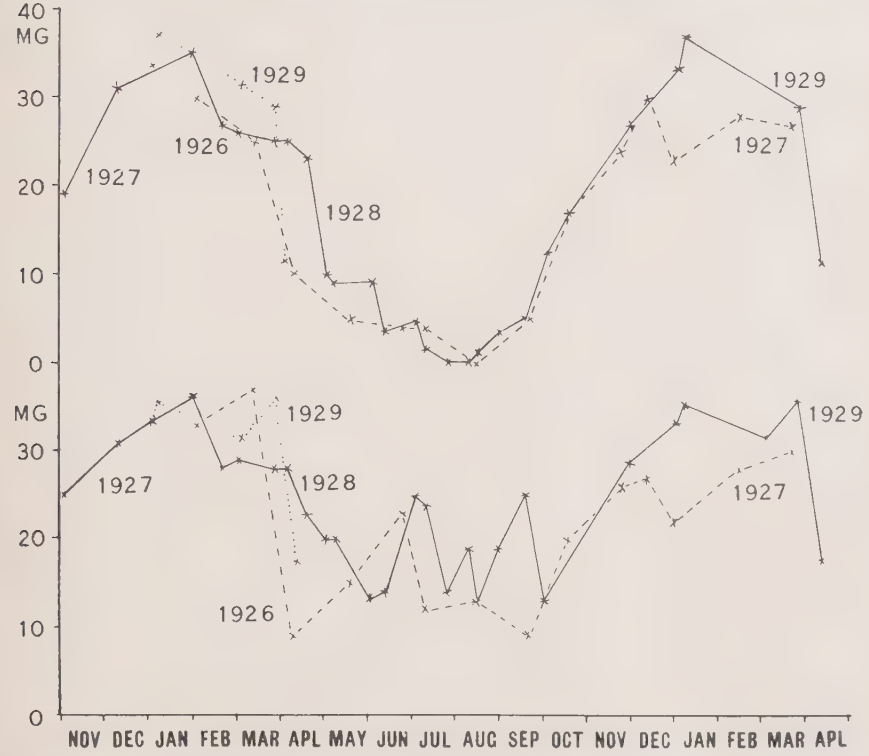

Fig. 2. Seasonal variation of phosphate concentration at Station E1. The upper portion gives the values at 5 m. and the lower those at the bottom, 70 m. The periods concerned are February 1926–March 1927, and November 1927–April 1929. Data for 1929 appear twice on the graphs, to compare with winter 1927 and the springs 1926 and 1928. Phosphate is shown as mg. P_2O_5 per m^3. From data of Table 3 (Atkins, 1928) and Table 1, this paper.

never reaches the surface as free phosphate. Even during summer there is a slow mixing of surface and bottom water as is shown by the way the bottom temperature gradually creeps up.

Seasonal Variation in Phosphate Concentration of Water at International Hydrographic Stations E1, E2, and E3.

The positions of these stations are roughly as follows : E1, 10 miles S.W. of Eddystone Lighthouse ; E2, Mid-Channel ; E3, 7 miles W. of

TABLE 2.

PHOSPHATE AS MG. P_2O_5 PER M.^{3} AND TEMPERATURES AT STATIONS E1, E2, AND E3.

	1927 Nov. 4		1928 Feb. 21–22.			May 7–9.			Aug. 16–17.			1929 Jan. 7.		March 26–27.		
M	E1	E2	E1	Ec	E3	E1	E2	E3	E1	E2	E3	E1	E2	E1	E2	E3
0	19	22	27	11	23	9	7	10‡	34	14·5	4	40	48·5	4	27·5	29
5	20	30	27	24	—	9	7	—	1	0	4	37	39	29	31	26·5
10	—	—	—	—	—	10	8	13	0	0	2	—	—	30	31·5	26
15	—	—	—	—	—	22	17	18	6	1	2	—	—	—	—	—
20	—	—	—	—	—	18	20	25	5·5	4	26	—	—	—	—	—
25	—	—	—	—	—	18	—	26	17	16	29	—	—	31	—	—
30	—	—	—	—	—	19	19	—	17·5	16·5	—	—	—	—	—	—
40	—	—	—	—	—	—	—	—	—	19·5	—	—	—	—	—	—
50	—	—	—	—	—	—	—	—	12·5	—	30	—	—	34·5	—	—
60	—	—	—	—	—	—	—	—	—	27	—	—	—	—	—	—
70	25	—	28	—	—	19	—	—	13	—	—	35·5	—	36	—	26
80	*	29	*	25	—	*	21	—	*	27	—	*	37·5	*	31·5	—
100		*		*	25		*	28‡		*	29·5		*		*	26
0	13·8	13·4	9·7	10·2	10·3	12·5	12·3	11·9	16·0	16·9	16·6	10·1	10·6	9·2	9·4	9·8
5	13·5	13·5	9·5	9·9	10·3	12·2	12·2	11·9	15·8	16·7	16·6	10·2	10·7	8·7	9·3	9·8
10	—	—	9·5	9·9	—	10·9	12·2	11·9	15·8	16·7	16·5	—	—	8·7	9·3	9·8
15	—	13·5	—	—	—	10·3	10·9	11·7	15·7	16·2	16·0	—	—	8·7	9·3	—
20	—	—	—	—	—	10·3	10·7	11 4	14·9	15·5	13·9	—	—	—	—	—
25	—	13·5	9·5	9·9	10·3		10·6	11·0	12·7	13·5	12·7	—	—	—	—	—
30	—	—	—	—	—	10·2	10·6	11·0	12·7	13·4	12·7	—	—	—	—	—
40	—	—	—	—	—		—	—	—	13·3	12·6	—	—	—	—	—
50	—	13·5	9·5	—	—		10·5	—	12·7	13·1	12·6	—	—	—	—	—
70	13·5	—	9·5	—	—	10·2	—	—	12·9	—	12·3	10·2	—	8·6	—	—
80	*	13·5	*	9·9	—	*	10·5	—	*	13·1	—	*	10·7	*	9·3	—
100		*		*	10·3		*	11·0		*	12·2		*		*	9·8

Mid-way surface phosphate values:— Feb., E1–E2, 24: E2–E3, 8; May, E1–E2, 7: E2–E3, 10; Aug., E1–E2, 13·5: E2–E3, 3; Jan., E1–E2, 49: March, E1–E2, 18·5· E2–E3, 36·5.

‡ Silica 80 mg. surface and bottom.

Ushant. The observations at E2 and E3 are at too great intervals of time to enable one to study the changes as closely as at E1. It may be said, however, that in general conditions at E2 are much the same as at E1. There is evidence, however, that a spring phytoplankton outburst may originate at E2 before there are any signs of it at E1. Thus on February 21st, 1928, the phosphate concentration at the surface was reduced to 11 mg. at E2, and to 8 mg. half-way on towards E3. Again, on March 11th, 1926, the values 11 mg., 0 mg., 5 mg., and 7 mg., were obtained, respectively, half-way between E1 and E2, at E2, half-way on to and at E3. Also on February 15th, 1927, 13 mg. was found for E2. It may thus be seen that the rapid utilization of phosphate by the phytoplankton depends purely upon the local conditions and may arise far out at sea. It need not depend upon anything washed out from the land.

Furthermore, references are found in the literature to phytoplankton outbursts attributed by various authors to enrichment of the sea-water by river water. The latter is, however, as a rule, far poorer in both phosphate and nitrate than is sea-water in winter or early spring. In silicate alone is river water richer than sea-water, but silicate has never been shown to be a limiting factor in diatom production in sea-water, and in spring silicate is present in the sea in abundance. Pending the production of direct analytical evidence as to the correctness of this theory of enrichment by fresh water, the author is unwilling to regard it as correct, save in comparatively landlocked basins.

Station E3 may be low in phosphate down to 15 m., but the deeper colder water is never greatly depleted, since there is so much vertical mixing thereabouts and the depth is considerably greater than at E1 or E2.

The Rapid Regeneration of Phosphate in Winter and the Water of an Offshore Wind.

Rough weather prevailed before and after Christmas 1927, but on January 2nd, 1928, it seemed just possible to get to E1 for routine water samples and to measure submarine illumination in mid-winter. Now it so happened that a rather unusual condition was observed, there was a steep gradient in phosphate concentration along the inshore stations, from L1 near the Laboratory to E1, 22 miles out.

The water at the Breakwater, L2, was just three times as rich in phosphate as that at E1 ; one might have concluded that the fresh water was enriching the sea-water, but this obviously required that the sea-water at L2 must have been diluted with fresh water to a very great extent, the salinity at E1 being 35·34$^{o}/_{oo}$, rather a high value typical of

Atlantic water. It was found, however, that even at L1 the salinity was 30·29°/$_{oo}$.

TABLE 3.

PHOSPHATE AS MG. P_2O_5 PER M^3., PHOSPHATE IN STORED SAMPLES, TEMPERATURES AND SALINITY IN PARTS PER THOUSAND. BETWEEN JANUARY 2ND AND 7TH, 1929, THE PREVAILING WIND WAS OFFSHORE, MAINLY FROM N.E. AT THE BOTTOM OF THE TABLE SILICATE ANALYSES ARE SHOWN AS MG. SiO_2 PER M^3.

Jan.	m.	L1	L2	L3	L4	L5	L6	E1	Mid E1–E2	E2
2†	0	161	143	125	125	93	125	48	—	—
2	5	—	—	—	—	—	—	33·5	—	—
2	70	—	—	—	—	—	—	33·5	—	—
7¶	0	—	—	39	49·5	48	48	40	49	48·5
7	5	—	—	—	35	—	36	37	37	39
7	10	—	—	34	—	—	—	—	—	—
7	25	*	*	34	—	—	—	—	—	—
7	40			*	34	—	—	—	—	—
7	60				*	*	34·5	—	—	—
7	70						*	35·5	36	37·5
					PHOSPHATE IN STORED SAMPLES.					
2‡	0	—	—	360	310	150	52	46**	—	—
					TEMPERATURE.					
2	0	8·9	8·5	9·4	10·2	10·3	10·6	10·5	—	—
7	0	—	—	8·8	9·6	9·7	9·9	10·1	10·3	10·6
7	5	—	—	9·2	9·6	—	9·9	10·2	10·4	10·7
7	B	—	—	9·7	9·9	—	10·1	10·2	10·4	10·7
					SALINITY, °/$_{oo}$.					
2	0	30·29	—	—	—	—	—	35·34††	—	—
7	0	—	—	—	35·18	35·19	35·33	35·37	35·41	35·36
7	5	—	—	34·78	35·13	—	35·23	35·37	35·35	35·33
7	B	—	—	35·03	35·21	—	35·28	35·35	35·35	35·37
					SILICA.					
2	0	870‡‡	686‡‡	466	246	190	217	183	—	—

† Jan. 2nd analysed Jan. 4th. ¶ Jan. 7th analysed Jan. 9th. ‡ Jan. 2nd analysed again on Jan. 9th. ** 70 m. sample gave 37 mg. * Bottom reached before depth indicated. †† Isohaline column. B, denotes bottom. ‡‡ Subject to a correction for tint in water, but as they stand they agree well with results in Table 1 of Atkins, 1926, p. 92, when latter are corrected by new factor.

This remarkable phosphate gradient was, moreover, shown to be a surface phenomenon only at E1 on January 2nd.

Between January 2nd and 7th the prevailing wind was offshore, mainly from the N.E. Under these conditions the fishermen at Plymouth say that it is almost useless to fish, as nothing worth while is caught. The idea prevails that the water is then very clear. On January 2nd photo-electric measurements did not show any exceptional clearness, and at E1 the Secchi disc could only be seen 9 m. down, as against a

maximum of 22 m. The 9-m. value is probably somewhat low, perhaps even as much as 3 m.—for the sea was very rough, with a heavy easterly swell. It was thought that the high phosphate concentration near the coast would give an indication as to whether surface water was being blown out to sea and replaced by deeper water moving nearer inshore. Accordingly on January 7th, the weather being exceptionally cold, temperature, phosphate and salinity depth series were worked from L3 to E2, as shown in Table 3. From L4 to E2 the surface phosphate was closely the same, save for E1, which was lower. Furthermore, the whole water column was somewhat richer at E2 than at the stations nearer land. Again the salinity results show a uniform Atlantic water from E1 to E2, and at L6, surface, with only very slight dilution. 3 parts in 1000 at L6, 5 m., and very little more at L4 throughout the water-column. There is therefore no evidence whatever that any extensive movement of the surface water was occasioned by the prevailing offshore wind or that the high values for phosphate in the surface waters were in any way connected with the wind. They arose through the decomposition of material rich in phosphate floating up to the surface all over the area studied, though the possibility is not precluded that a certain amount of seaweed and particulate matter may drift out to sea through wind action. Further evidence of enrichment through decomposition is offered by the fact that certain of the water samples taken on January 2nd and stored till January 9th gave even higher values than when freshly drawn.

A Comparison of the Phosphate Content of the Water at E1 in Different Years.

In Table 4 the mean values of the phosphate content of the water-column are shown, from 1923–1929. There is usually a maximum in January. For the seven years the mean maximum was 35·1 mg., varying from 37·0 to 31·0 mg. Very strangely there were mid-winter phyto-plankton outbursts in mid-December 1925 and late December 1926.

The minimum values for the water-column were found in June, July, or August, with secondary minima in April or May. For the five summers studied the mean minimum was 7·6 mg., varying from 8·7 to 5·1 mg.

The data are shown in Figure 3, the years being continued into the January following to show the winter maxima or depressions. The most striking thing about the curves, apart from their general similarity, is the rapid fall in the spring of each year. The fall, however, differs from year to year both as regards its date and its rate, as shown by the slope of the curve. Tables 5 and 6 have been prepared to facilitate the comparison of the years, as indicated in their headings. The dates are shown at which certain phosphate concentrations were reached at

TABLE 4.

PHOSPHATE CONTENT OF THE WATER-COLUMN, SURFACE TO BOTTOM, 70 M., AT STATION E1, EXPRESSED AS MG. P_2O_5 PER M^3. THE MONTHS ARE DIVIDED INTO THREE PORTIONS EACH, EQUAL IN LENGTH.

		1923	1924	1925	1926	1927	1928	1929
Jan.	I	—	*37·0*	—	—	21·6	—	*36·5*
,,	II	—	—	*31·9*	*40·0**	—	—	—
,,	III	—	—	—	—	*36·2*	—	—
Feb.	I	—	—	—	33·0	—	—	—
,,	II	—	32·0	31·1	—	27·9	27·8	—
,,	III	—	—	—	—	—	—	—
Mar.	I	*37·0*	—	—	36·4	—	28·5	31·5
,,	II	—	22·1	28·3	—	29·0	—	—
,,	III	—	—	—	—	—	25·8	31·4
April	I	—	15·0	—	—	—	25·6	—
,,	II	—	—	—	9·5	—	23·1	14·4
,,	III	27·7	—	8·5	—	—	—	—
May	I	—	—	—	—	—	17·2	—
,,	II	—	12·1	9·2	12·9	—	—	—
,,	III	11·6	—	—	—	—	—	—
June	I	—	—	15·8	—	—	10·6	—
,,	II	13·2	9·1	—	—	—	**8·3**	—
,,	III	—	—	—	16·0	—	—	—
July	I	—	**8·7**	6·9	10·5	—	13·7	—
,,	II	**7·4**	—	—	—	—	14·2	
,,	III	—	—	—	—	—	10·2	—
Aug.	I	—	10·1	19·2	—	—	9·4	—
,,	II	16·1	—	—	10·4	—	12·0	—
,,	III	—	—	—	—	—	15·3	—
Sept.	I	—	16·1	**5·1**	—	—	—	—
,,	II	13·9	—	—	—	—	19·0	—
,,	III	—	—	—	**8·6**			
Oct.	I	—	14·9	18·2	—	—	12·8	—
,,	II	16·0	—	—	18·2	—	—	—
,,	III	—	—	—	—	—	—	—
Nov.	I	20·0	—	—	—	23·5	—	—
,,	II	—	20·1	25·9	—	—	—	—
,,	III	—	—	—	25·6	—	27·9	—
Dec.	I	—	32·0	—	—	*31·0*	—	—
,,	II	34·0	—	18·6	29·8	—	—	—
,,	III	—	—	—	21·6	—	34·0	—

* This is really a surface value for L6, but L3–L6 gave the same value for phosphate, but it may possibly be too high for E1. Weather was too bad to get to E1 or to do the depth series.

surface and bottom, also the temperatures of the water on those dates. Both dates and temperatures are then compared with those of the first year of the series, 1923. Now the phosphate depletion is a measure of

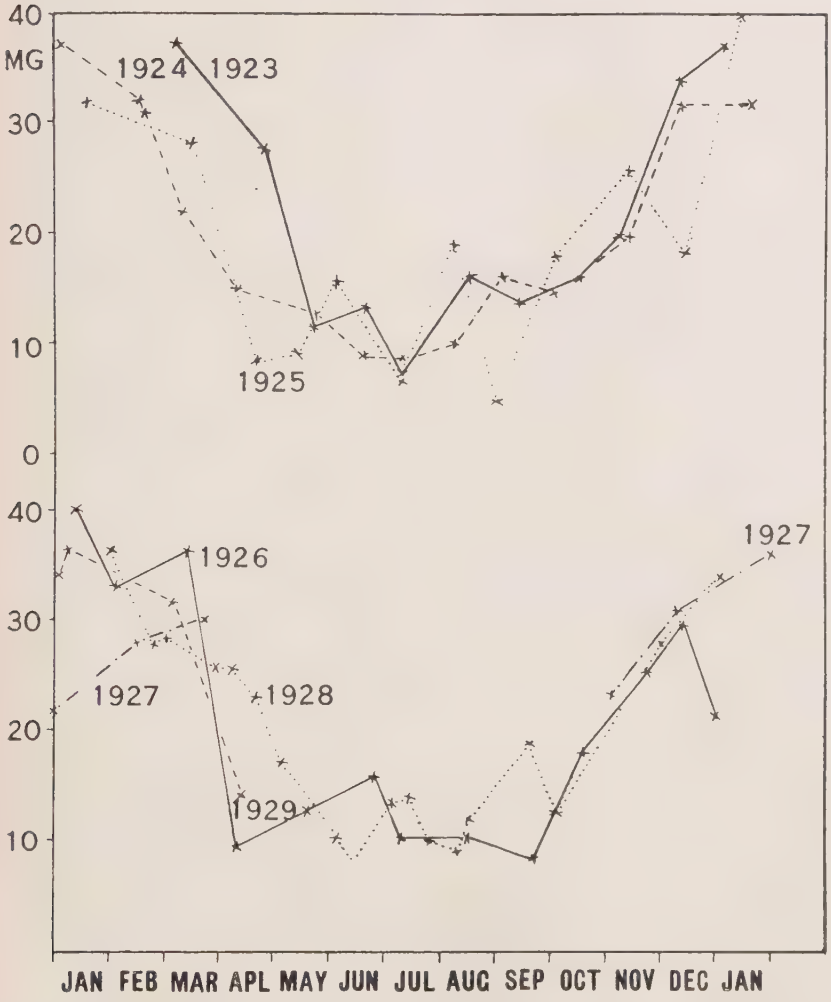

FIG. 3. Mean phosphate concentration of the whole water-column, 70 m., at Station E1 expressed as mg. P_2O_5 per m^3. The upper portion shows the values throughout the years 1923, 1924 and 1925, the lower those for 1926, portions of 1927, 1928 and the spring of 1929. From data of all papers of the series, and Table 4.

the phytoplankton production, which is only secondarily affected by temperature. The latter has been included mainly on account of its influence upon the rate of hatching of fish eggs and upon the rate of growth of animals.

TABLE 5.

DATES AND TEMPERATURES WHEN CERTAIN PHOSPHATE CONCENTRATIONS WERE REACHED AT E1, SURFACE. TAKING THE 1923 DATES AND TEMPERATURES AS ARBITRARY STANDARDS THE ADVANCES OR RETARDATIONS OF THE OTHER YEARS ARE RECORDED IN DAYS AND DEGREES.

mg.	1923	1924	1925	1926	1927	1928	1929	1924	1925	1926	1927	1928	1929
30	March 30	Feb. 18	Feb. 25	Feb. 3	Feb. 6	Feb. 13	March 18	41	33	55	52	46	12
30	9·7°	8·4°	9·6°	9·5°	9·2°	9·5°	8·9°	−1·3°	−0·1°	0·2°	−0·5°	−0·2°	−0·8°
20	April 28	Feb 28	March 20	March 21	—	April 22	April 4	59	39	38	—	6	24
20	10·2°	8·0°	9·4°	9·7°	—	10·4°	9·0°	−2·2°	−0·8°	−0·5°	—	+0·2°	−1·2°
10	May 10	April 28	April 6	April 10	—	May 2	April 13	12	34	30	—	8	27
10	11·0°	9·4°	9·5°	10·2°	—	11·4°	8·8°	−1·6°	−1·5°	−0·8°	—	+0·4°	−2·2°
2·5	May 21	June 18	April 18	July 21	—	July 6	—	−28	33	−61	—	−46	—
2·5	11·4°	13·7°	9·7°	17·0°	—	14·7°		+2·3°	−1·7°	+5·6°	—	+3·3°	—
2·5	Sept. 15	Aug. 24	Sept. 10	Sept. 6	—	Aug. 25	—	+22	5	+9	—	+21	—
2·5	15·0°	15·0°	16·0°	16·9°	—	16·0°		0·0°	+1·0°	+1·9°	—	+1·0°	—
10	Sept. 28	Oct. 20*	Oct. 6	Oct. 3	—	Sept. 28	—	−22	−8	−5	—	0	—
10	14·0°	12·9°	14·3°	15·9°	—	15·5°		−1·1°	+0·3°	+1·9°	—	+1·5°	
20	Nov. 7†	Nov. 22	Nov. 1‡	Nov. 6	Nov. 6	Nov. 5	—	−15	+6	−1	−1	−2	—
20	12·2°	12·3°	12·6°	13·3°	13·7°	13·6°		+0·1°	+0·4°	+1·1°	+1·5°	+1·4°	—
30	Dec. 1	Dec. 6	Jan. 2§	Dec. 12	Dec. 3	Dec. 14	—	−5	−32	−11	−2	−13	—
30	10·9°	11·9°	10·2°	11·7°	12·1°	11·4°		+1·0°	−0·7°	+0·8°	+1·2°	+0·5°	

* Also on Sept. 2, giving +26. † Also on Oct. 11. ‡ Also on Dec. 21. § 1926.

TABLE 6.

DATES AND TEMPERATURES WHEN CERTAIN PHOSPHATE CONCENTRATIONS WERE REACHED AT E1, BOTTOM. TAKING THE 1923 DATES AND TEMPERATURES AS ARBITRARY STANDARDS, THE ADVANCES OR RETARDATIONS OF THE OTHER YEARS ARE RECORDED IN DAYS AND DEGREES.

mg.	1923	1924	1925	1926	1927	1928	1929	1924	1925	1926	1927	1928	1929
30	April 14	Feb. 20	March 17	March 17	March 21	Feb. 17	April 1	54	28	28	24	57	13
30	9·6°	8·6°	9·2°	9·5°	9·0°	9·4°	8·7°	−1·0°	−0·4°	−0·1°	−0·6°	−0·2°	−0·9°
20	May 9	March 17	April 11	March 27	—	May 2	April 9	53	28	43	—	7	30
20	10·2°	8·0°	9·4°	9·5°		10·2°	8·8°	−2·2°	−0·8°	−0·7°	—	0·0°	−1·4°
15	May 20	April 9	April 26	April 2†	—	May 25	April 14	41	24	48	—	−5	36
15	10·4°	8·3°	9·5°	9·5°	—	10·8°	8·9°	−2·1°	−0·9°	0·9°	—	+0·4°	−1·5°
15	Oct. 20*	Aug. 15	Sept. 19§	Oct. 6‡	—	Oct. 9§§	—	66	31	14	—	+11	—
15	13·2°	12·1°	13·0°	14·6°	—	14·4°	—	−1·1°	−0·2°	+1·4°	—	+1·2°	—
20	Nov. 6	Nov. 4	Sept. 29	Oct. 18	—	Oct. 28	—	2	38	19	—	9	—
20	12·3°	12·9°	13·5°	14·5°	—	13·5°	—	+0·6°	+1·2°	+2·2°	—	+1·3°	—
30	Dec. 1	Dec. 4	Dec. 28	—**	Dec. 3	Dec. 8	—	−3	−27	—	−2	7	—
30	11·0°	11·9°	10·5°	—	12·2°	11·8°	—	+0·9°	0·5°				

It may be seen that 1924, 1926 and 1929 are early years, 1928 being late, with 1923 even later. The differences are, moreover, very striking since 1924 and 1926 are 6 to 7 weeks ahead of 1923 and 1928. The earliest spring, 1924, happened also to be the coldest, both at the time of the vernal outburst and in general. It must accordingly have been

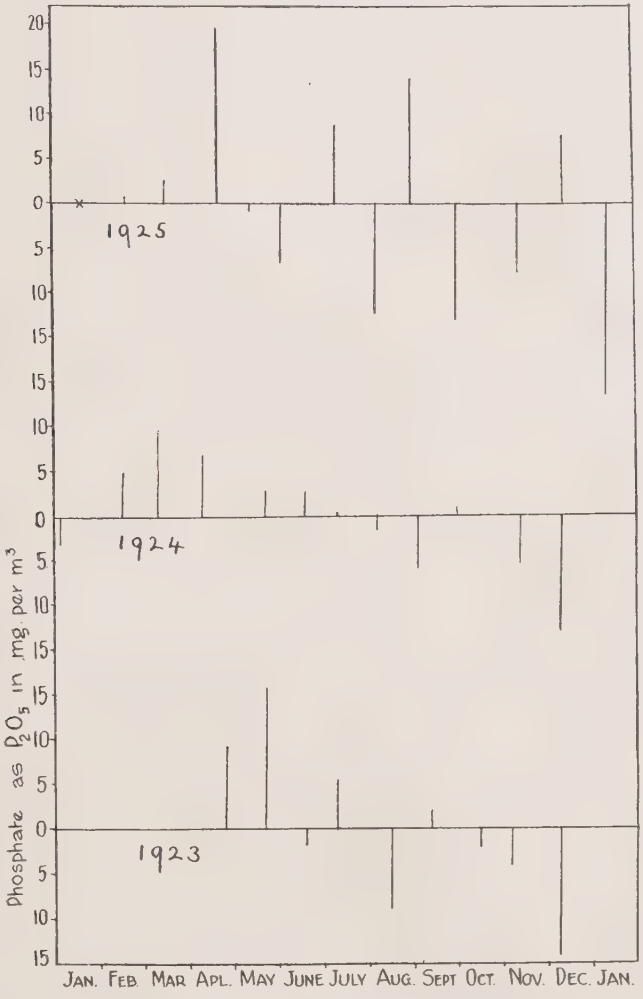

FIG. 4. The production of phytoplankton, at Station E1, may be deduced from the uprights above the zero line; in reality these lines show the difference in the mean phosphate concentration of the water-column, expressed as mg. P_2O_5 per m^3., between two successive observations. Decrease in phosphate, being equivalent to production of phytoplankton, is shown above the zero line. From data of Table 3 (Atkins, 1926).

[Reprinted from Fig. 4, *Jour. Mar. Biol. Assoc.*, 1926, **14**, 454.]

one in which the hatching of fish eggs went on most slowly. This year therefore should be an outstanding one as regards suitability or otherwise for various species of young fish. The next year to 1924 as regards low temperature was 1929, a moderately early year, though not as early as 1924 or 1926—or even as 1925 as regards the surface.

The autumnal regeneration of phosphate seems to proceed rather more

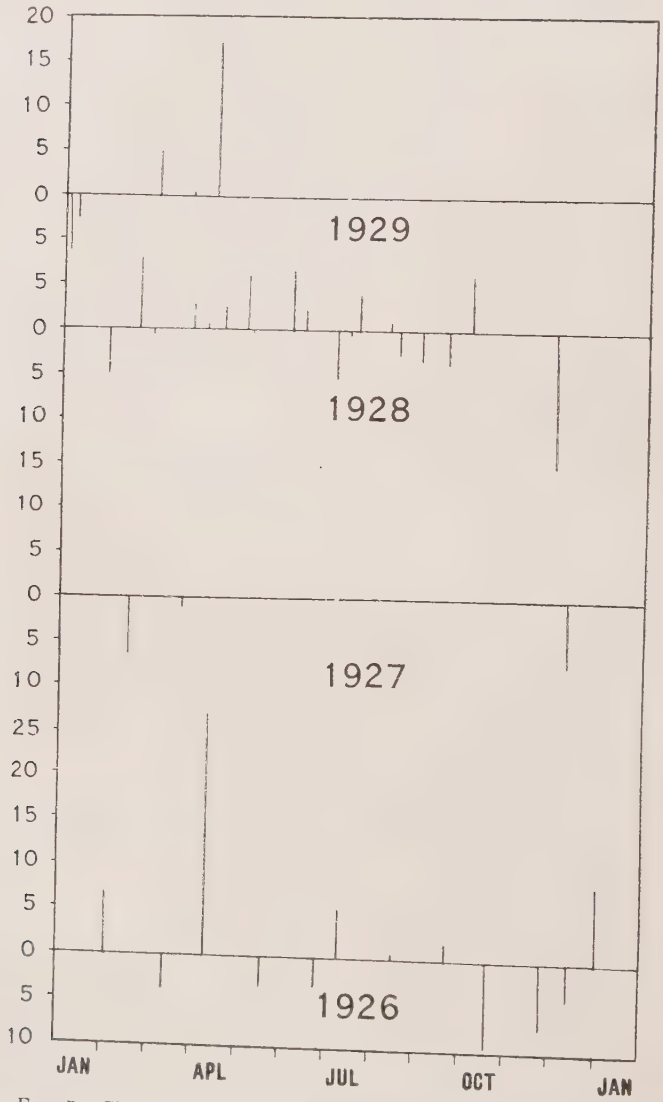

FIG. 5. Similar to Fig. 4, but for years 1926–1929, spring. From data of Tables 4 and 7.

regularly as to date and temperature than does the vernal consumption process.

It is possible to make further use of the data of Table 4, which gives the mean phosphate concentration of the water-column, because the differences between consecutive values are a measure of the consumption or regeneration of phosphate. Such differences are shown in Figures 4 and 5 as perpendiculars above or below the zero line, erected at distances on the abscissæ corresponding to the date of the second of each pair of analyses.

In comparing these two figures it is obvious that the height of a perpendicular depends to some extent on the frequency of the observations. The diversity of the years is, however, brought out very clearly. Thus the two late years, 1923 and 1928, are in some respects quite different; 1928 began as a rather early year but did not maintain its productivity; 1924 began very early and its further progress, both as regards production of phytoplankton and regeneration of phosphate, was monotonously regular. In 1925 large outbursts were followed by periods of very considerable regeneration; both 1925 and 1926 had December outbursts; 1926 and 1929, as well as 1925, had single spring outbursts of remarkable magnitude.

During 1928 analyses were performed at shorter intervals in connection with the work on illumination. It may be seen in Figure 5 that the first perpendicular above the line is followed by a very small one below it, the second above the line by a third above it, but very small. There are further on two very small perpendiculars below the line in May and July. Obviously the rates of production of phytoplankton varied greatly. Table 7 shows such rates in terms of consumption or regeneration of phosphate, the latter being denoted by a plus sign; these were obtained as described in the heading of the table, and are shown in Figure 6, the construction of which is given in the legend.

The phenomenon that is brought out most clearly in Figures 4, 5, and 6 is that production of phytoplankton is not a process that proceeds uniformly at a slow rate, or at an ever-increasing rate, till limited by lack of phosphate. Such a deficiency does ultimately limit it, but in between productivity proceeds in a series of bounds, with periods of no change of rate or with periods of decay in between. Since phosphate consumption is never very great below 25 m. at E1, in the absence of vertical mixing, this depth has been selected as one above which the main region of photosynthesis lies. The illumination at 25 m. is from about 1·0 to 10·4 per cent of full daylight. Vertical mixing, however, introduces complications, especially as the main spring outburst occurs before the formation of the epithalassa. Moreover, in autumn, at the end of September or very early in October, the resumption of vertical

TABLE 7.

THE UPPER PORTION OF THE TABLE SHOWS PHOSPHATE CONCENTRATION, IN MG. P_2O_5 PER M.^{3}, AT STATION E1, AVERAGED FROM 0–70 M., ALSO FROM 0–25 M. AND 25–70 M., TOGETHER WITH THE DIFFERENCES, △, BETWEEN CONSECUTIVE OBSERVATIONS. THE LOWER PORTION GIVES THE INTERVALS BETWEEN THE OBSERVATIONS, THE RATES OF PHOSPHATE CONSUMPTION OR REGENERATION, IN MG. P_2O_5 PER M.^{3} PER DAY, AND THE MEAN DATES FOR WHICH THE RATES ARE TAKEN AS APPLICABLE.

Date.	4/11/'27	9/12	31/1/'28	21/2	1/3	27/3	5/4	19/4	2/5	7/5	4/6	13/6
0–70 m.	23·5	31·0	36·2	27·8	28·5	25·8	25·6	23·1	17·1	17·3	10·6	8·3
△	—	+ 7·5	+ 5·2	− 8·4	+ 0·7	2·7	− 0·2	− 2·5	− 6·0	+ 0·2	− 6·7	− 2·3
0–25 m.	21·0	31·0	36·5	27·4	28·1	25·4	24·9	23·2	12·2	14·5	9·0	4·5
△	—	+10·0	+ 5·5	− 9·1	+ 0·7	− 2·7	− 0·5	− 1·7	−11·0	+ 2·3	− 5·5	− 4·5
25–70 m.	24·9	31·0	36·0	27·9	28·7	26·0	27·0	23·0	19·9	19·0	11·5	11·1
△	—	+ 6·1	+ 5·0	− 8·1	+ 0·8	− 2·7	+ 1·0	− 4·0	− 3·1	− 0·9	− 7·5	− 0·4
Interval, days	—	35	53	21	9	26	9	14	13	5	28	9
Mean date	—	21/11	4/1	10/2	25/2	14/3	31/3	12/4	25/4	4/5	21/5	8/6
Rate, 0–70 m.	—	+0·21	+0·10	−0·40	+0·08	−0·10	−0·02	−0·18	−0·46	+0·04	−0·24	−0·26
Rate, 0–25 m.	—	+0·29	+0·10	−0·43	+0·08	−0·10	− 0·06	−0·12	− 0·85	+0·46	−0·20	−0·50
Rate, 25–70 m.	—	+0·17	+0·10	−0·39	+ 0·09	−0·10	+ 0·11	− 0·29	−0·24	− 0·18	−0·27	− 0·04

TABLE 7 (*continued*).

4/7	11/7	23/7	9/8	16/8	29/8	18/9	2/10	30/11	2/1/'29	7/1	4/3	26/3	11/4
13·7	14·2	10·2	9·4	12·0	15·3	19·0	12·8	27·9	34·0	36·5	31·5	31·4	14·4
+ 5·4	+ 0·5	− 4·0	− 0·8	+ 2·6	+ 3·3	+ 3·7	− 6·2	+15·1	+ 6·1	+ 2·5	− 5·0	− 0·1	−17·0
4·8	3·6	4·2	1·3	7·6	11·4	8·1	12·4	27·0	35·0	37·3	31·5	27·4	12·3
+ 0·3	− 1·2	+ 0·6	− 2·9	+ 6·3	+ 3·8	− 3·3	+ 4·3	+14·6	+ 8·0	+ 2·3	− 5·8	− 4·1	−15·1
18·6	20·1	13·6	13·8	14·4	17·4	25·0	13·0	28·3	33·5	36·0	31·5	33·7	15·6
+ 7·5	+ 1·5	− 6·5	+ 0·2	+ 0·6	+ 3·0	− 7·6	−12·0	+15·3	+ 5·2	+ 2·5	− 4·5	+ 2·2	−18·1
21	7	12	17	7	13	20	14	59	33	5	56	22	16
23/6	7/7	17/7	31/7	12/8	22/8	8/9	25/9	31/10	16/12	4/1	4/2	15/3	3/4
+0·26	+0·07	−0·33	−0·05	+0·37	+0·25	+0·18	−0·44	+0·26	+0·19	+0·50	−0·09	−0·05	−1 06
+0·01	−0·17	+0·05	−0·17	+0·90	+ 0·29	−0·17	+0·31	+0·25	+ 0·24	+0·46	−0·10	−0·19	−0·94
+0·36	+0·21	−0·54	+0·01	+0·09	+0·23	+0·38	−0·86	+0·26	+0·16	+0·50	−0·08	+ 0·10	−1·13

mixing may cause the upper 25 m. to show a gain in phosphate, indicating apparently a period of regeneration, whereas the whole water-column may show a reduction in phosphate, as on October 2nd, 1928. For these reasons, the values for the whole column are the most reliable, though the other two have been tabulated for the information they can yield

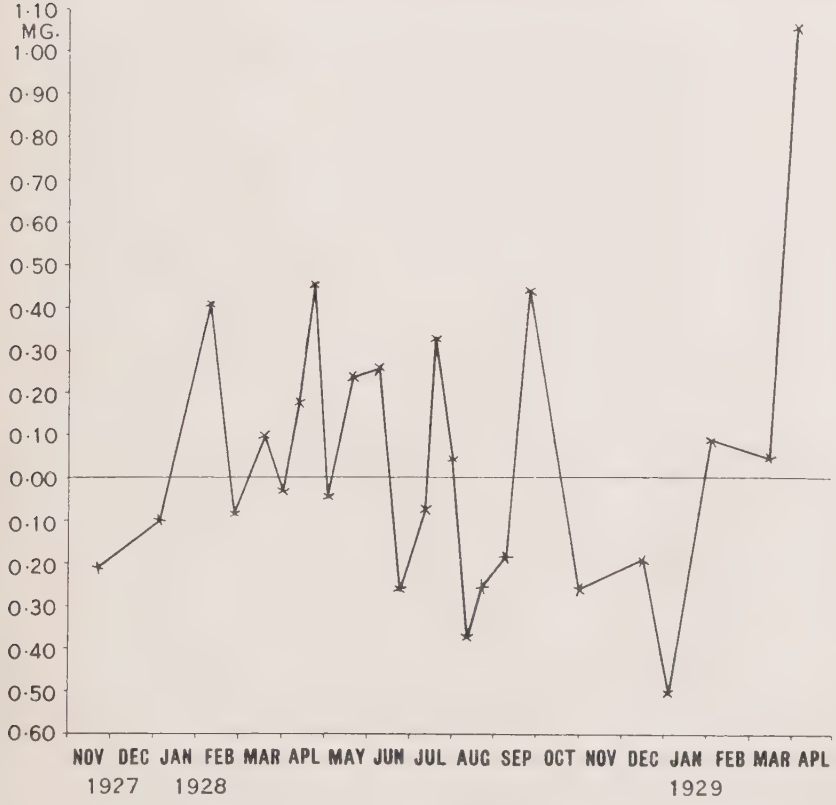

FIG. 6. The ordinates represent mg. P_2O_5 per m^3. per day, and denote the rates of change in phosphate concentration at Station E1, throughout the whole 70 m. water-column. The rates are plotted for the dates midway between those on which the water was sampled. Decrease in concentration, being equivalent to increase in phytoplankton, is plotted above the zero line. The crests are therefore times of maximal rates of production of phytoplankton, the troughs of maximal rates of decay of phyto- and zoo-plankton combined. From data of Table 7.

when considered in relation to the possible sources of error in their interpretation. The maximum consumption rate found for the whole column was 1·06 mg. P_2O_5 per $m.^3$ per day, for April 3rd, 1929, followed by 0·46 for April 25th, 1928, 0·44 for September 25th, 1928, and 0·40 for February 10th, 1928. Such rates would soon reduce the phosphate content to zero were they to be continued. For the upper 25 m. the

maxima were 0·94 for April 3rd, 1929, 0·85 for April 25th, 1928, 0·50 for June 8th, 1928, and 0·43 for February 10th, 1928. The greatest rate of all was observed in the lower region, 25–70 m., when vertical mixing was active, namely, 1·13 mg. for April 3rd, 1929, followed by 0·86 for September 25th, 1928, and 0·54 for July 17th, 1928.

The writer is indebted to Mr. H. W. Harvey for the construction of isohalines which show that there was no marked influx of water into the mouth of the English Channel during the period studied. It is accordingly legitimate to regard the cyclic processes at E1 as being those taking place in a closed system.

A Comparison of the Variation in Hydrogen Ion Concentration, Total Carbon Dioxide and Phosphate Content of Sea-water.

An extended series of measurements of the hydrogen ion concentration was made some years ago in order to obtain an estimate of the minimum weight of the phytoplankton crop from the change in the carbon dioxide content as shown by alteration in alkalinity. This was abandoned as the phosphate analyses gave the desired information more simply. It was intended, however, to institute a comparison of the two, but a few series only could be made in 1928. These are shown in Table 8, besides similar observations for 1922. When arranged in order of the monthly dates the two years are seen to agree closely, as might be expected if made in the same year.

TABLE 8.

Hydrogen Ion Concentration, pH value, of Sea-water at Station E1, Determined Colorimetrically at Sea upon freshly drawn Samples using Cresol Red and McClendon's Buffer Solutions. Comparison of Autumn 1922 with 1928.

m.	Sept. 18th, 1928.	Sept. 22nd, 1922.	Oct. 2nd, 1928.	Oct. 12th, 1922.
0	8·24	8·22	8·22	8·20
5	8·24	8·22	8·22	8·20
10	8·23	8·22	—	8·20
15	—	8·21	8·22	8·20
20	8·21	8·21	—	8·20
25	8·19	8·20	8·22	8·20
30	8·15	8·18	—	8·20
40	8·15	8·18	—	8·20
70	8·14	8·18	8·22	8·20

A comparison of the changes in phosphate and in carbon dioxide is shown in Figure 7, constructed as indicated in the legend. It may be

seen the vernal fall in carbon dioxide and in phosphate are rather similar, both are reduced during the summer, and rise in winter, though the high value of the previous winter was not reached by the carbon dioxide by January 1924. The figure makes it clear that though the phosphate is greatly reduced, in summer, throughout the whole water-column—to

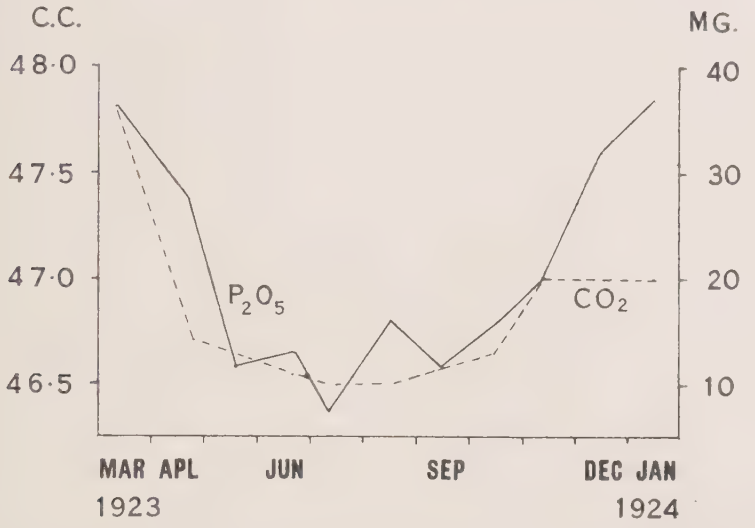

Fig. 7. The left-hand ordinates denote cubic centimetres of carbon dioxide per litre, those on the right mg. of P_2O_5 per m^3. The phosphate values are those for the whole water-column for the period shown by the abscissæ. The carbon dioxide values, broken line, denote the total amount present in the water-column, in c.c. per litre—the water being of alkaline reserve "26," namely, requiring 26 c.c. of N/10 HCl to neutralize one litre at 100° C. The carbon dioxide was found by converting the pH (logarithmic) values obtained, with cresol red and McClendon's standards (Atkins, 1924), into concentrations, cH values, for each depth, and from these a mean value for the water-column was got and converted into the pH value. From the pH values for the various dates, McClendon's (1917) curve for excess base 26 was used to read off the c.c. of CO_2 per litre. Author indebted to H. W. Harvey for this figure.

about 25 per cent of its winter value, yet the reduction in carbon dioxide is comparatively small, from 47·8 to 46·5 c.c. per litre.

The Silicate Content of Sea-water and its Seasonal Variation.

Table 1 shows the silicate at Station E1, expressed as mg. SiO_2 per m^3. The results have been plotted in Figure 8, surface full line and bottom broken line. For comparison a dotted curve shows phosphate, at 5 m. There is a general agreement between the curves, but the silicate curve never reaches zero. It does, however, reach a minimum of 33 in July,

which is about the limit of what is definitely detectable by the method. The surface silicate is, during the summer, rather lower than the bottom concentration. The sudden rise in the latter in September is probably associated with movement of water in from slightly further out. Of this there is definite hydrographic evidence. It is also noteworthy that whereas the phosphate one winter is closely the same as that in the following winter, when at its maximum, yet the 1928–1929 silica concentration was far below that of 1927–1928. Furthermore, in April 1928 the steep fall in silica took place some weeks before the marked fall in phosphate. This looks as if the latter was due in the main to a Phæocystis

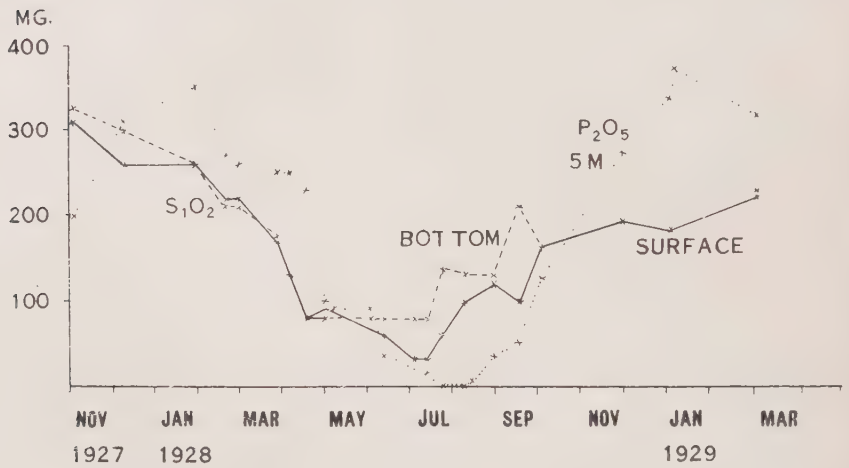

FIG. 8. The ordinates represent silicate, as mg. SiO_2 per m^3., the abscissæ show months The full line curve is that for surface water, the broken line representing concentrations found in bottom samples. For comparison a dotted curve has been given to show phosphate concentrations, as mg. P_2O_5 per m^3., at 5 metres—to avoid surface irregularities due to regeneration. For this curve the ordinate scale readings must be reduced to one-tenth to read miligrams.

outburst, and the later complete exhaustion of phosphate, when silica was increasing, may possibly have been due largely to the growth of Peridinians. In the absence of a proper examination of the plankton it is impossible to decide such questions.

Table 3 furnishes additional support to the finding of a previous year as to the steep silicate gradient existing near the land.

The Phytoplankton at Station E1.

Lack of a collaborator has rendered it impossible to make regular and approximately quantitative observations on the phytoplankton and to correlate them with the changes in phosphate concentration as Marshall

and Orr (1927) have done in the Clyde. It was found, however, that *Phæocystis globosa* occurred abundantly in the tow-nets on May 2nd, 1928, the date on which the fall in phosphate concentration was also found (Table 1), temperature 10·2–11·4° C. On April 4th, 1929, every sample of water obtained by the Nansen-Pettersen bottle from surface to bottom contained Phæocystis in abundance. This also coincided with the

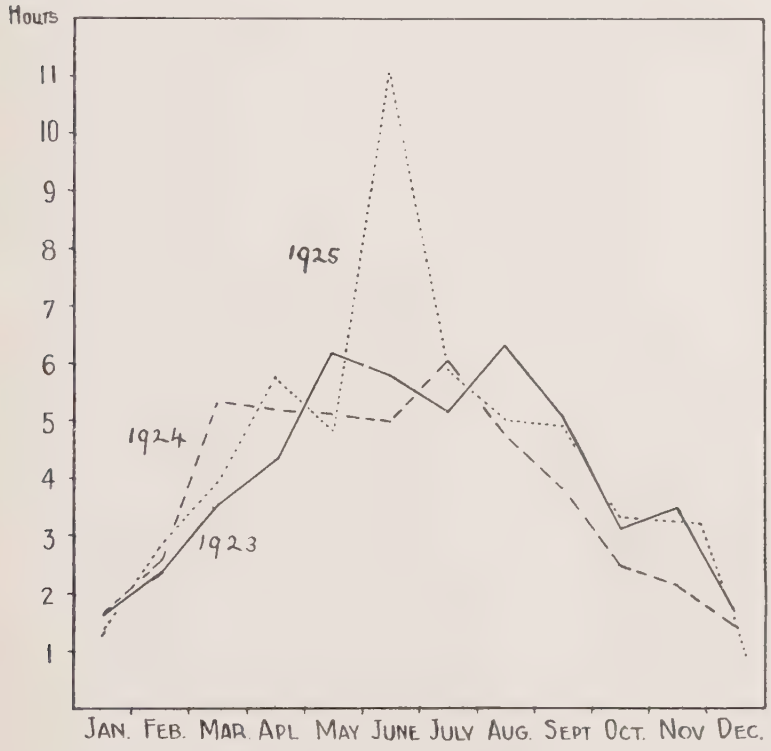

FIG. 9.—Mean monthly sunshine records, in hours per day, for England S.W. (including S. Wales), plotted for 15th of each month, 1923–1925. From Meteorological Office Records.

[Reprinted from Fig. 5 of *Jour. Mar. Biol. Assoc.*, 1926, **14**, 457.]

sudden fall in phosphate, which took place about a month earlier than in 1928, the temperature being 8·8°. Next in abundance to Phæocystis the water from the sample bottles, examined directly, without centrifuging, with a low power in a small dish, contained the following: *Lauderia borealis*, abundant; *Rhizosolenia stolterfothii*, a fair amount; *Chætoceros decipiens*, frequent; *Nitzschia delicatissima*, embedded in the jelly of Phæocystis, a small species of Gymnodinium; *Navicula membranacea*, also occasional cells of *Rhizosolenia shrubsolii*, *R. robusta*, *Skeletonema*

costatum, *Chætoceros densus*, *C. sociale*, Navicula sp., *Nitzschia closterium*, *Streptotheca tamensis*, *Hyalodiscus stelliger*, Thalassiosira sp., Pleurosigma sp., *Peridinium ovatum*, *P. pentagonum*, Dinophysis sp., *Spirodinium spirale*. The water-column being isothermal the plankton was

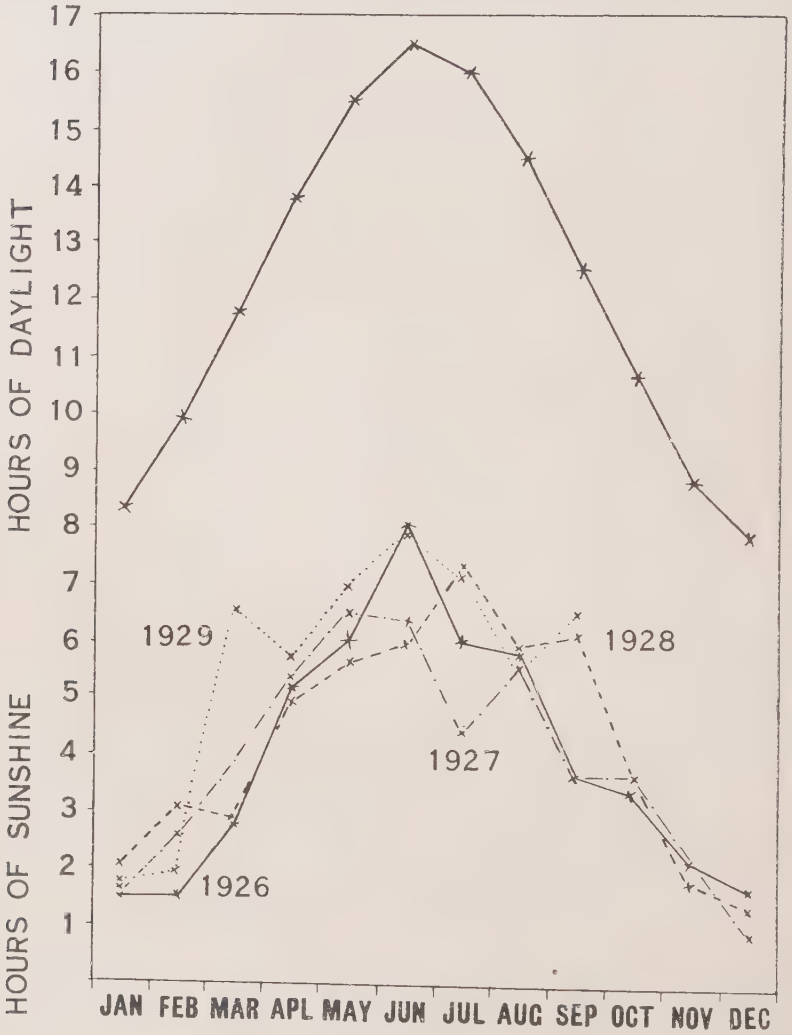

Fig. 10. As Fig. 9, 1926–1929, also mean length of daylight per day, for each month, plotted for 15th.

well distributed but seemed more abundant at 15 m. than elsewhere. The phosphate concentration was slightly lower at 5 and 10 m. than elsewhere. I am indebted to Dr. M. V. Lebour for kindly identifying the phytoplankton.

The Causes of the Difference in the times of Phosphate Consumption from Year to Year.

In an earlier paper (1926) it was shown that the years 1924 early, 1925 intermediate, and 1923 late were arranged in the order of their early spring sunshine records, as may be seen in Figure 9. A similar agreement had been found by Herdman, Scott and Dakin (1910), 1907 having an unusually early diatom crop, following, with a lag, a high value for February sunshine. Marshall and Orr (1927), however, found a remarkable constancy in the date of the vernal outburst in the Clyde area. Their phosphate estimations were checked by counting the diatom chains, a good agreement being found. In another paper (1928) the E1 observations concerning the years 1923, 1924 and 1925 were shown to be associated with predominant north-sector winds in 1924. The relation works back to the sunny weather and clear skies associated with northerly winds.

Figure 10 is similar to Figure 9, but concerns 1926–1929 ; 1926 has been classed as an early year, like 1924, but Figures 4 and 5 show that in detail the years were very different, for 1924 gave a regular series of productivity uprights, whereas in March 1926 regeneration preponderated, being associated with 2·8 hours sunshine per day. The big outburst came in April, with an average of 5·2 hours sunshine per day. After this 6 hours daily in May and 8 hours in June did not lead to the complete exhaustion of the phosphate, though the surface values were further reduced. The epithalassa having become established regeneration took place, but very low phosphate values were found in July, August and September, even with decreased sunlight. One has, however, to consider the possible effect of variations in the clearness of the water, data on which are recorded in Table 1 and are shown in Figure 11. These variations are such as to alter the illumination about eight times, much the same as is found between a dull winter day giving 15,000 metre-candles and a very bright summer or spring day with 120,000 m.c. So unless one knows the absorption coefficient it does not follow that a period of bright sunshine is necessarily one of high illumination at, say, 15-25 m., though it will probably be so at depths down to 10 m. in the open sea.

The year 1927 should have been an earlier year than 1926, with 3·9 hours daily sunshine for March. Observations up to March 21st, after which they are lacking, showed no outburst, but rather slow regeneration till March, following upon the small and unusual outburst at the very end of December 1926.

The year 1928 was studied in great detail. There was a moderate outburst late in February with small ones in the end of March and middle

of April and larger ones early in both May and June, causing the year to be grouped with 1923 as late, though it began well in February; in this month the sunshine was 116 per cent of the normal, January having had 125 per cent. That for March was only 73 per cent, and April 89 per cent.

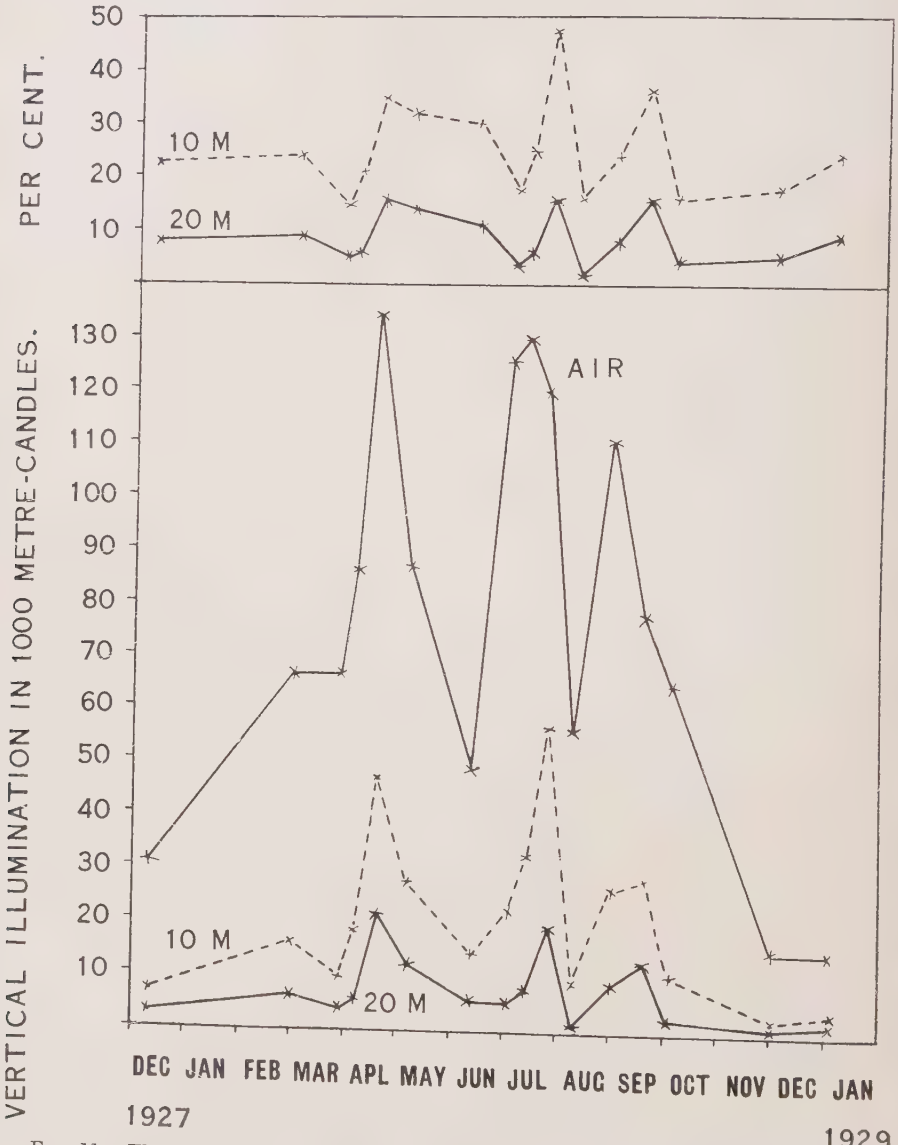

FIG. 11. The upper portion represents the percentage of the vertical illumination (received on a horizontal surface) penetrating to 10 and 20 metres, at Station E1, on the dates shown. The lower portion gives the vertical illuminations, in 1000-metre-candles, in air, at 10 and at 20 m. Data from Poole and Atkins (1929).

In 1929 the most striking feature was the great outburst early in April. After an almost normal January sunshine (104 per cent) and only 75 per cent of the normal in February, that for March had risen to 165 per cent, 6·54 hours per day. This seems obviously connected with the early April outburst. Figure 11 also shows the mean monthly length of the day for the meteorological district, namely, England S.W. and

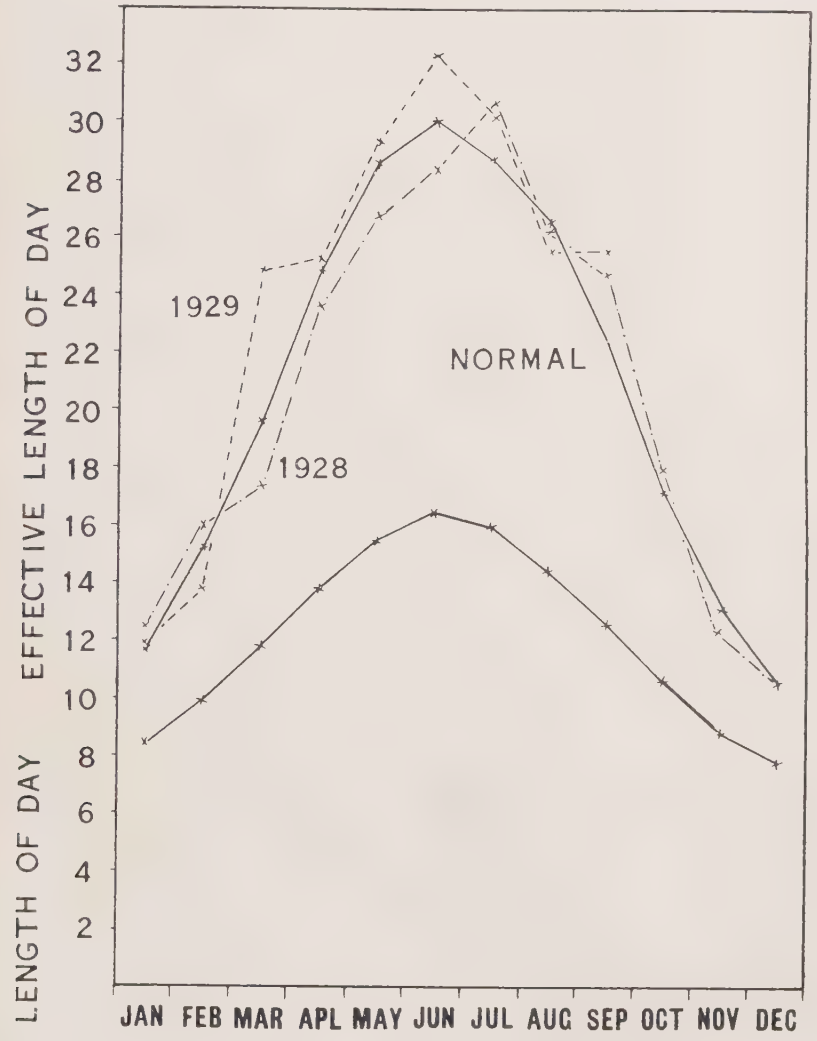

Fig. 12. The lowermost curve shows the length of day in hours for the meteorological district England S.W. (including S. Wales). The upper full curve shows the normal "effective" length of day for the district, counting each hour of sunshine as equivalent to two hours of diffuse light. (See text.) The curve with dot and dash shows the "effective" length of day for 1928; the curve with dashes only represents 1929.

S. Wales. It is obvious that length of day is a very important factor as regards the causation of an outburst of plant growth. Poole and Atkins (1929) found that the vertical illumination due to the sun's direct rays is about twice as great as that due to the diffuse light. Thus sunshine, which usually occurs in the midday hours, has the effect as it were of trebling the duration of the light, when at its highest, for in addition to a normal diffuse light of, say, 30,000 m.c. there will be an extra 60,000 due to sunlight; this is equivalent to three times as long at 30,000 m.c. Since, however, the sunshine hours are already included in the length of the day we can get a rough idea of the "effective length of day" by adding, to the mean length for the month, twice the mean monthly sunshine for the month of the year under consideration. This gives an approximate relative figure for the same months of different years; thus for March the normal "effective" length of day is 19·7 hours for the district, whereas that for 1928 was 17·6 and for 1929 it was 24·9 hours. The comparison is only a rough one, however, for the different months, because the average diffuse illumination varies greatly from month to month; also the sunlight is not twice as powerful as the diffuse light in the depth of winter and is more than twice as powerful in mid-summer. Figure 12 shows the mean monthly length of day for the district, also the normal "effective" length of day, obtained from the normal values of the mean monthly sunshine. The broken lines show the "effective" length of day for 1928 and 1929. The great difference in March appears to offer a rational explanation of the remarkable phytoplankton outburst early in April 1929. Pending the obtaining of accurate measurements of the daily or monthly illumination in metre-candle hours by means of a permanently exposed photo-electric cell and a Cambridge Instrument Co. "thread recorder," the curves of Figure 12 may serve as a rough approximation.

Estimation of Silicate.

As mentioned previously (1923, 1926) there is always a suspicion that a trace of silicate may dissolve from the bottle unless this has been waxed. The values given were obtained for the most part using samples from waxed bottles, but these were occasionally supplemented by analyses from the ordinary hard green glass bottles. The following values, in mg. SiO_2 per cubic metre, were obtained for E1, September 18th, 1928, analysed on 20th: 0 m., 99; 15 m., 100; 20 m., 102; 25 m., 163; 30 m., 118; 40 m., 144; 60 m., 209. Only the 0 m. sample was from a waxed bottle, but obviously the 15 and 20 m. samples agree well. The 25 m. sample is from water totally different as regards temperature and phosphate, but from this depth downwards both are almost uniform, whereas the silicate values are not. It seems possible that suspended

diatom tests and siliceous material has been dissolved in varying amount, but the glass risk is not excluded; the tints are moreover so faint that too great reliance must not be placed in the analytical results. The degree of accuracy attainable may be judged from the following analyses of samples from E1, July 23rd, 1928, using waxed bottles: taking 100 mg. and 200 mg. standards the surface results were 55 and 60 mg. respectively and the bottom 142 and 130 mg. Nevertheless, it seems likely that such accuracy is not always obtained.

A matter of greater importance is the picric acid used in making up the standard solution, for which 36·9 mg. of picric acid has been taken as corresponding to 50 mg. p.l. of SiO_2 in solution as silicate according to Diénert and Wandenbulcke (1923). Thresh and Beale (1925) used 40 mg. of picric acid. King and Lucas (1928), however, state that 25·6 mg. of vacuum-dried, C.P. picric acid per litre gives a colour equivalent to 50 mg. p.l. of SiO_2 with the reagents. They suggest that possibly the earlier workers neglected to dry the picric acid, to which water is usually added for safety. My own standard solution was made from picric acid crystals which had been for several years in a nearly empty bottle and appeared to be quite dry; they were further dried over sulphuric acid in a desiccator. The crystals used by Thresh and Beale were also dried over sulphuric acid in an ordinary desiccator (private communication). It seems unlikely that so large a discrepancy can be accounted for merely by the difference in drying in an ordinary and a vacuum desiccator, yet the work of King and Lucas, carried out with every precaution and with picric acid recrystallised from benzene (Benedict, 1922), renders it desirable that the standards used by different workers should be compared till uniformity is secured.

As first pointed out by Folin and Doisy (1916), impure picric acid, specially common at about that time, may be a source of error in estimating creatine and creatinine. A rather laborious purification gave a product that could be relied upon, though Benedict (1922) reported samples that were not even improved by this repetition of recrystallization of sodium picrate from water. Benedict found that recrystallization of even the "technical" grade of picric acid from hot benzene gave a product which was quite satisfactory. The impurities give a deep colour with alkali; this is important in the creatine estimation, but affects the silica estimation far less, since it is carried out by comparison with an acid mixture. Recently, however, Benedict (1929) has found samples of picric acid which show little improvement after crystallization from benzene. He recommends the use of glacial acetic acid as a solvent for the dried picric acid, or alternatively recrystallization of the sodium salt by a modification of the Folin-Doisy method, using sodium carbonate instead of sodium hydroxide.

Through the courtesy of Dr. E. J. King it is now possible to be sure that analyses on opposite sides of the Atlantic are truly comparable. He examined my standard picric acid solution and found that it agreed exactly with his own, made up to be 36·9 mg. per litre. This, according to Diénert and Wandenbulcke, is equivalent in colour to one containing 50 mg. SiO_2 per litre. According to King and Lucas this is matched by 25·6 mg. of picric acid per litre. Apparently the fault lies in the picric acid originally used by Diénert, for the silica content of silicate can readily be checked by gravimetric analysis. Since in my earlier work I used Diénert and Wandenbulcke's factor, all the figures published must be multiplied by 1·30. Those given in this paper *are now correct by King's standard.*

Methods of Calculating the Allowance to be made for the Reagent Blank.

The analyses of phosphate were made, as heretofore, by the coeruleo-molybdic method of Denigès, using 100 c.c. of liquid in a Hehner tube. The allowance for the reagent blank is of course a perfectly general correction, necessary in all colorimetric work involving minute quantities.

The blank correction was formerly made as follows: if using as standard a 0·05 mg. per litre solution of phosphate, reckoned as P_2O_5, or 50 mg. per cubic metre, 100 c.c. of distilled water plus reagents matches 10 c.c. of standard plus reagents. The amount of the blank then corresponds to $\frac{50\times10}{100}=5$. This amount corresponds to a full column, therefore if an unknown solution matches at a reading of 40, it is clear that the standard column contains two-fifths of the blank in excess of its supposed phosphate content, whereas the unknown contains the full amount of reagents producing the blank. Accordingly three-fifths of the blank must be subtracted from the apparent amount found for the unknown, namely,

$$\frac{50\times40}{100}=20, \text{ less } 3=17.$$

This, however, is not quite correct, for the real strength of the standard has been increased by the presence of the reagents also. In general terms let k denote the true amount of the blank, c the concentration of the standard before addition of the blank-producing reagents, x the reading for the blank and y that for the unknown solution containing an amount z: then

$$k=(c+k)\times\frac{x}{100},$$

$$\text{and } z+k=(c+k)\times\frac{y}{100}$$

Now taking, as before, x=10 and y=40, with c=50 mg. per cubic metre, we get :—

$$100\,k=500+10\,k, \text{ hence } k=5{\cdot}5$$

$$\text{and } z+k=\frac{55{\cdot}5\times 40}{100}=22{\cdot}2$$

hence z=16·7, as against z=17 by the approximate correction. In view of the fact that a difference of two units on the scale corresponds to 1 mg. per cubic metre, the use of the approximate correction is not a cause of any appreciable error. However, using a weaker standard solution the error may become more serious, especially for higher values of k and lower values of y.

Thus, with k as before, viz. 5·5, y=40 and c=25, we get

$$z+k=\frac{30{\cdot}5\times 40}{100}=12{\cdot}2,$$

whence z=6·7 and the approximate method gives :—

$$z=\frac{c\times 40}{100}-\frac{60}{100}k,$$

hence z=10—3=7, which is in good agreement. However, with x=24, and c=25 we get k=6·0 by the approximate method and 7·9 by the exact one. With these values and y=30 the approximate method gives 3·3, the exact 2·0. An alternative approximation, in cases where y approaches to x, is to subtract and calculate from :—

$z=\frac{(y-x)c}{100}$, which with the above assigned values gives z=1·5, which would then be rounded off to z=2 as obviously nearer than z=1.

Since in the present paper the interest lies partly in seeing how near to complete exhaustion the phosphate content may go, it has seemed advisable to use the first approximate method when c=50, as before, and to adopt the exact formula for use with the very weak solutions estimated with standard c=25 mg. per cubic metre.

SUMMARY.

1. The phosphate content of sea-water at Station E1 ranged, during the period November 1927–April 1929, from 48 mg. P_2O_5 per m^3., to 0·0 mg. The former was an exceptional and temporary surface value during phosphate regeneration in mid-winter ; the latter was a very usual value at from 0–15 m. during July, August or even September.

2. For the whole water-column, 0–70 m., at E1 the maximum values were 36·2 and 36·5 mg. during the winters 1927–1928 and 1928–1929 respectively. The minimum value for the column was 8·3 mg. in June 1928.

3. For the seven years 1923–1929 the maximum value for the phosphate content of the whole column was 37·0 mg. in 1923 and 1924, the lowest winter maximum observed being 31·0 mg. For the seven years the mean maximum value was 35·1 mg. The five summers gave a mean minimum value of 7·6 mg. for the column, the absolute minimum being 5·1 mg. on August 31st, 1925.

4. Additional evidence has been obtained that the surface may be a region of phosphate regeneration, not only in winter, but in bright summer weather when apparently the illumination is too intense for diatoms to thrive. Normally the bottom and deeper waters are the chief sites in which regeneration becomes apparent.

5. Taking the vernal consumption of phosphate as a standard, the years 1924, 1926 and 1929 were early years, 1928 being late with 1923 even later. The differences may amount to as much as 6 or 7 weeks. The earliest spring, 1924, happened also to be the coldest. It must accordingly have been one in which the hatching of fish eggs went on most slowly. This year, therefore, should be an outstanding one as regards suitability or otherwise for various species of young fish.

6. The differences in the seasonal productivity of the various years is well brought out by erecting perpendiculars, at the proper positions on the time abscissæ, which are proportional to the differences between successive observations of the phosphate concentration of the water-column. It is seen that the production of phytoplankton, as measured by phosphate consumption, proceeds by a series of outbursts.

7. The rate of production throughout the whole water-column was as much as 1·06 mg. P_2O_5 per m^3. per day for April 3rd, 1929. For the upper 25 m. the maximum rate found was 0·94 mg. for the same date, with 1·13 mg. for the column from 25–70 m. Owing to vertical mixing with surface water poorer in phosphate this rate is fictitiously the greatest.

8. A comparison of the total carbon dioxide content of the water-column at various times during the year has shown that in a general way the minimum is reached at about the same time as the phosphate minimum. The carbon dioxide content was found to vary from 47·8 to 46·5 c.c. per litre, so it never remotely resembles complete exhaustion in the open sea.

9. There is a general agreement between the curves for seasonal variation in phosphate and in silicate, but the latter never reaches zero. The July minimum for the surface, 33 mg. SiO_2 per m^3. is very near the limit of what can be detected. The winter maxima differ more than do the phosphate maxima from year to year, that for 1927–1928 and 1928–1929 being respectively 320 and 220 mg. A sharp fall in silica content in the spring may be several weeks ahead of a similar fall in phosphate.

10. The factor for silica determination as given by King and Lucas has been adopted in preference to that of the originators of the method of colorimetric comparison against picric acid. This necessitates the multiplication of the results of my analyses, published heretofore, by the factor 1·30. The trouble has apparently been due to the presence of an impurity in the picric acid used by Diénert which may render advisable a method of purification recognised as necessary in the determination of creatine and creatinine.

11. In April 1929 a sudden fall in phosphate concentration was accompanied by a remarkably rich phytoplankton outburst. Every sample of water bottled from 0–70 m. contained lumps of Phæocystis jelly, as well as the diatom *Lauderia borealis* in abundance, though not so in every sample. *Rhizosolenia stolterfothii*, *Chætoceros decipiens*, and *Nitzschia delicatissima* were also plentiful; twelve other species of diatoms were found and four of the Peridineæ.

12. The order in which the years stand in § 5 is, in a general way, the order of spring sunshine. The variations in the clearness of the water must be taken into account in assessing the submarine illumination; such variations may cause an eight-fold variation in the upper 20 m., much the same as is found between winter and spring.

The length of the day as well as the sunshine is important in regulating the amount of photosynthesis. Crediting the day with two hours extra daylight for each hour of sunshine a graph has been constructed which shows how 1929 was in this respect ahead of 1928 in the spring. The comparison is a fair one for the same months of different years, but only rough for the different months, as the sun's altitude varies.

It should be added that the values quoted for the salinity of the water were determined in the Government Chemists' Laboratory, London.

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A Study of the Spring Diatom Increase in Loch Striven.

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With 15 Figures in the Text.

The spring diatom increase in the open sea and probably also in inshore waters is one of the most important annual biological events and information regarding it or its causes is likely to be of value. In an inshore area changes are not only more pronounced, but also take place more rapidly than in the open sea and, for this reason among others, the increase was studied in Loch Striven, a well-sheltered loch in the Clyde Sea Area. A general description of the weekly changes occurring in this loch has already been made (Marshall and Orr, 1927). The changes during the spring, however, are so rapid that an examination at even closer intervals during this period was thought advisable. Such an examination was made in 1927 and 1928, the interval between successive visits being generally two days. The methods used were the same as those described in the above-mentioned paper.

During the spring increase in Loch Striven in the years studied the sea was an almost pure culture of *Skeletonema costatum*. The other diatom species which occurred were few enough to be negligible and animal life was scarce. Before the increase began Skeletonema formed over 96% of the diatoms. On March 19th, 1928, of the first thousand cells counted, only five cells were not Skeletonema, on the 22nd less than 10, and on the 26th only 13. Thus the changes occurring were due almost entirely to one diatom species.

The spring increase of 1926 has been described in the paper referred to (Fig. 7). Visits were made only about once a week and the depths worked were 0, 5, 10, 20 and about 30 fathoms. The increase was regular in form, beginning at the surface and sinking gradually into

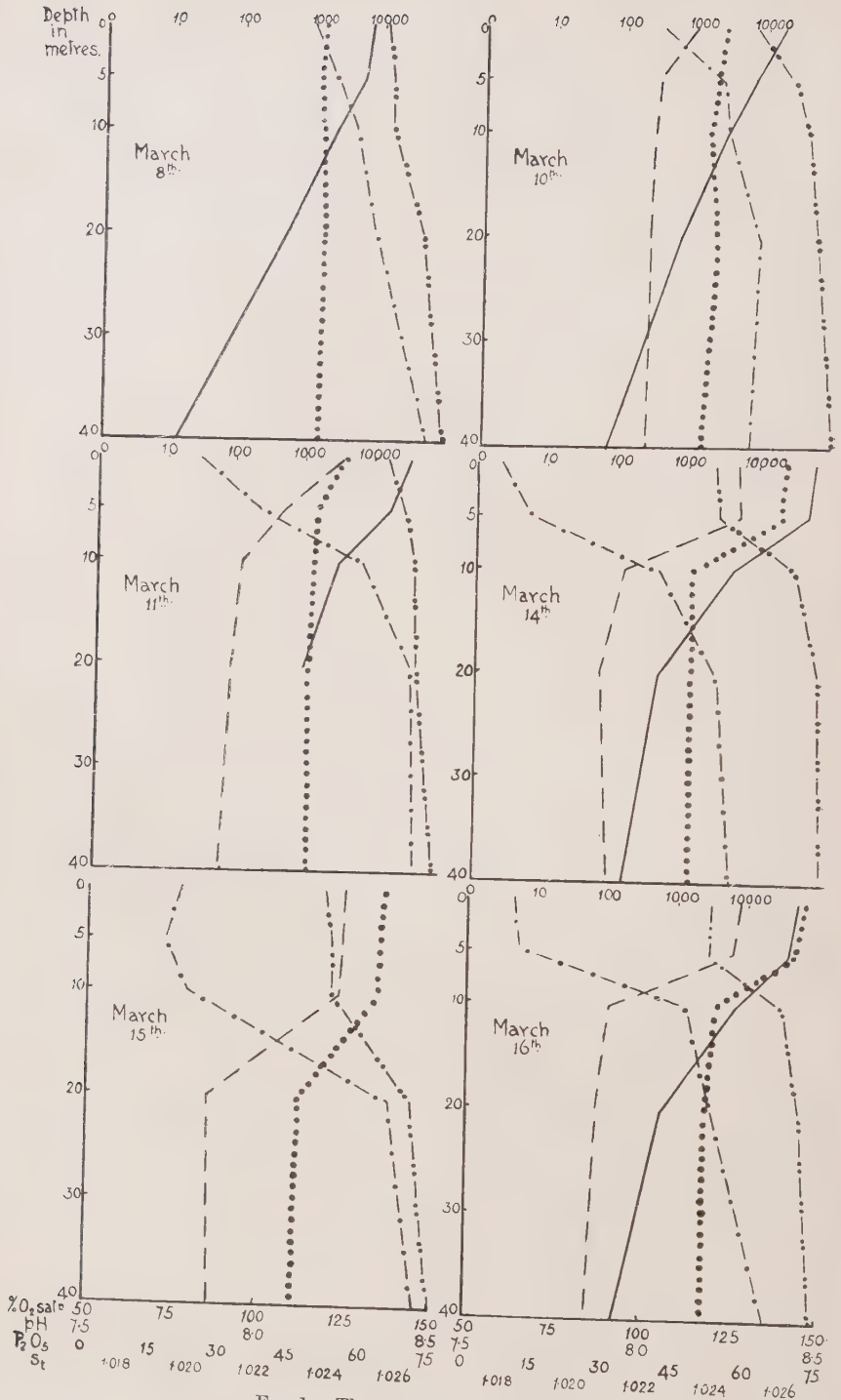

FIG. 1.—The spring increase in 1927.

——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — . . — . . S_t.

deeper water, so that the maximum at 5 fathoms occurred the week after the maximum at the surface, and the maximum at 10 fathoms a week later. After this the fall was rapid, showing that the diatoms had sunk below the depth to which photosynthesis was possible. Three weeks after the beginning of the increase the diatoms had almost disappeared from the loch. The chemical factors showed a similar series of changes, the pH value and oxygen content rising and the phosphate falling with an increase in diatom numbers.

In 1927 (see Figs. 1, 2, 3 and 8, and Table 1) the loch was visited more frequently and the depths worked were 0, 5, 10, 20 and 40 metres. The increase had started before the first visit was made on March 8th and there were more than 5000 diatom chains per 20 c.c. in both surface and 5-metre samples. This is an unusually early increase when compared with previous years. The diatoms had increased again on the 10th, and between the 10th and the 11th the numbers were doubled at the surface (16,700 to 33,100) and 5 metres (6900 to 16,400). This very rapid change was accompanied by a sharp rise in oxygen saturation (110% to 121%), a slight rise in pH value and a marked fall in dissolved phosphate. In the deeper water, however, there was also a considerable change, the phosphate and dissolved oxygen saturation values being different from that for the 10th. This leads one to suppose that the change was not due entirely to diatom growth, but that the water examined was not the same as on the previous day. That such an increase can take place naturally, however, is shown by Gran (1927).

At this time the surface density was lower than that of the other layers so that no vertical mixing was going on. On the 14th a fall in density at surface and 5 metres stabilised the loch still further and the chemical changes were correspondingly more marked. The diatoms also reached their maximum for the increase and were almost as numerous at 5 metres (51,000) as at the surface (62,700), but this is probably due to the mixing of the waters between these depths.

On the 15th there was a hard S.E. wind and the effect of this was similar to that described by Murray for some Scottish lochs (1888) and by Gran and Gaarder (1918) for the Oslo fiord. The surface waters were piled up in the loch so that the values found the previous day at surface and 5 metres were now found at surface, 5 and 10 metres. Diatoms were not counted this day, but it is almost certain that the high figures would have been found at 10 metres also. On the 16th and 17th conditions had returned to normal and were very much the same as on the 14th. By the 18th diatoms were very much more numerous at 5 metres than at the surface in spite of the fact that the density at these depths was much the same. This shows that the diatoms have begun to sink and this process had gone still further by the 22nd when the maximum numbers

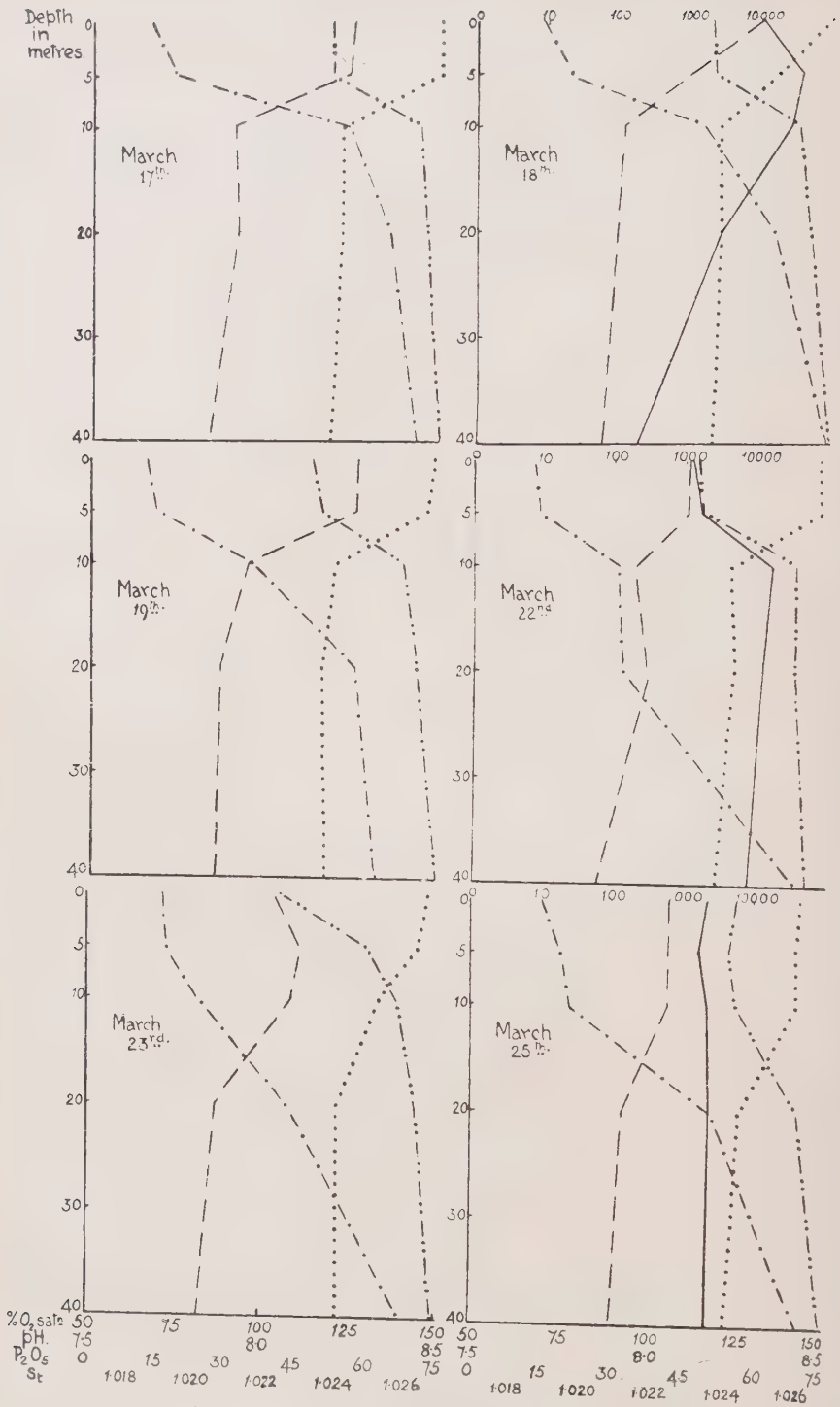

FIG. 2.—The spring increase in 1927 (contd.).

——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — .. — .. S_t.

were found from 10 to 40 metres. By the 25th numbers at all depths had fallen and the increase was over. There are no chemical changes corresponding to the high diatom numbers at and below 20 metres, which indicates that the diatoms are sinking passively and that no photosynthesis is going on there.

An examination of the loch at intervals of about two days shows that the regularity of the increase is not so marked as when the examination is made only once a week. These irregularities are partly because in an enclosed area the effect of wind and tide is much more marked than in the open sea. Another point of interest is that the increase falls off before all

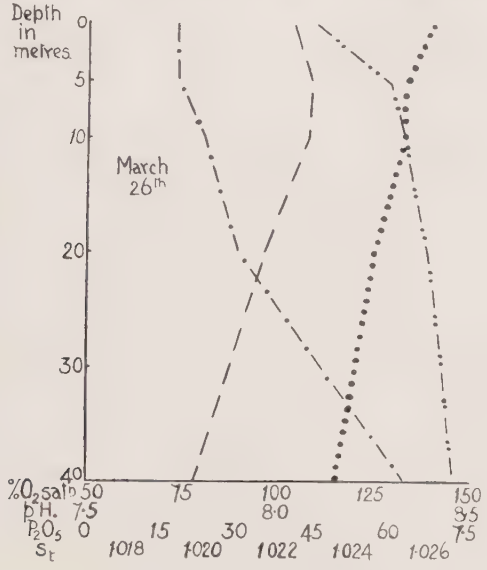

Fig. 3.—The spring increase in 1927 (contd.).
——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — .. — .. S_t.

the phosphate is utilised, which is at variance with the results obtained in the open sea (Atkins, 1926), but is in agreement with the results obtained during the spring increase in the same loch in 1926. No other essential nutrient salts were estimated, however, and it is possible that one of these may have been limiting. There is, nevertheless, a definite relationship between the chemical factors and the diatoms. Estimation of small quantities of phosphate is not very exact when diatoms are very numerous, for they then give the sample a brownish tinge which interferes somewhat with the blue colour given by the phosphate reagent.

In 1928 (see Figs. 4, 5, 6 and 9, and Table 2) the number of diatoms was estimated by counting the cells and not the chains. Several counts

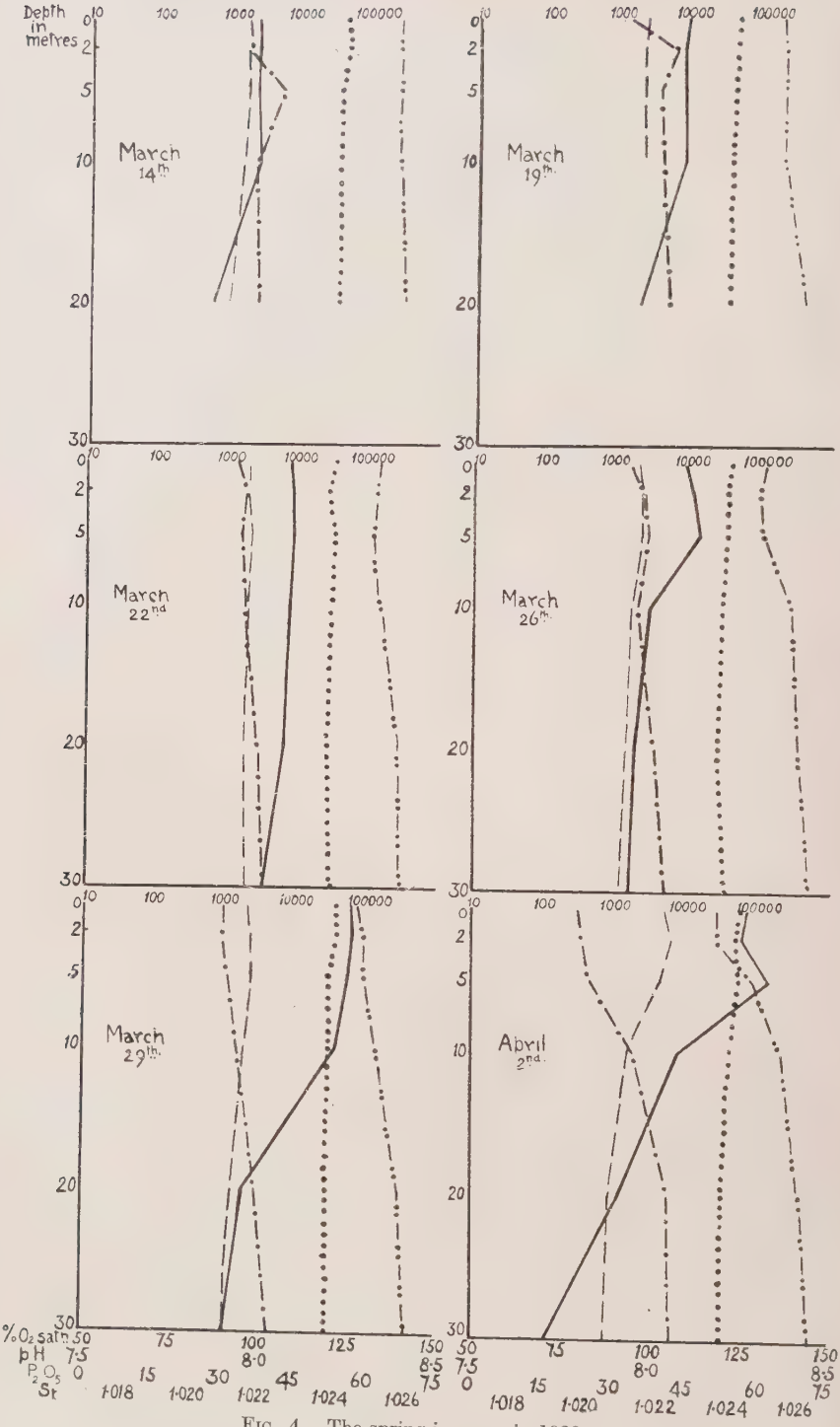

FIG. 4.—The spring increase in 1928.

——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — .. — .. S_t.

gave an average of about 10 cells per chain and this figure held till the end of the increase when it fell somewhat. They were counted in this way to bring the work into line with that done elsewhere, and the comparison with 1926 and 1927 can be made by multiplying the figures for those years by 10. Gran (1929) estimates that the number of cells in a chain of *Skeletonema costatum* is 16 or more. The reason for the difference may be that our samples were centrifuged living and not after preserving. The depths worked were 0, 2, 5, 10 and 20 metres. The additional depth of 2 metres was chosen because the maximum amount of photosynthesis may not occur at the surface.

On March 14th there were already between two and three thousand cells per 20 c.c. down to a depth of 10 metres. This is higher than normal for winter, and a certain amount of growth must have been going on. The pH value was also higher than the normal winter value. By March 19th numbers had increased at all depths counted but were still much the same, 7000 to 8000 from 0 to 10 metres. Values for density, oxygen saturation, pH and phosphate show the same conditions. The temperature overturn had not yet taken place and the loch was therefore in an unstable condition in which vertical mixing was possible. Conditions were much the same on the 22nd, but mixing, and along with it, diatom numbers had spread deeper. The increase had progressed considerably by the 26th and diatoms were fairly rich (9000 cells at the surface, 11,300 at 2 metres, 13,500 at 5 metres). At the same time, however, density was almost uniform to 5 metres so that this distribution is apparently not due to a real sinking of the diatoms but to vertical mixing to this depth. The chemical changes also agreed with density. By the 29th the temperature had risen at the surface, the loch was in a more stable condition, and there was a great increase in the number of diatoms down to 10 metres. The values for the chemical factors, however, showed little alteration. On April 2nd the loch was supersaturated with oxygen down to 5 metres and the phosphate values had fallen as far as the same depth. The diatom distribution was irregular, rising as far as five metres, then falling sharply in the deeper water. Two days later, on April 4th, density had fallen again at the surface and there was a steep gradient from there down to 10 metres. Corresponding with this phosphate had fallen to zero at the surface, the oxygen saturation had risen to 115% and pH value had also risen, while the diatoms had multiplied still further and were richer in the 2-metre sample (248,000) than at the surface (180,000). Since the loch was now quite stable, this is probably a real sinking and not caused simply by mixing.

On April 6th the loch remained stable, the diatoms had fallen to 5 metres where they reached their maximum number for this increase (510,000 cells in 20 c.c.), the oxygen saturation had also reached its

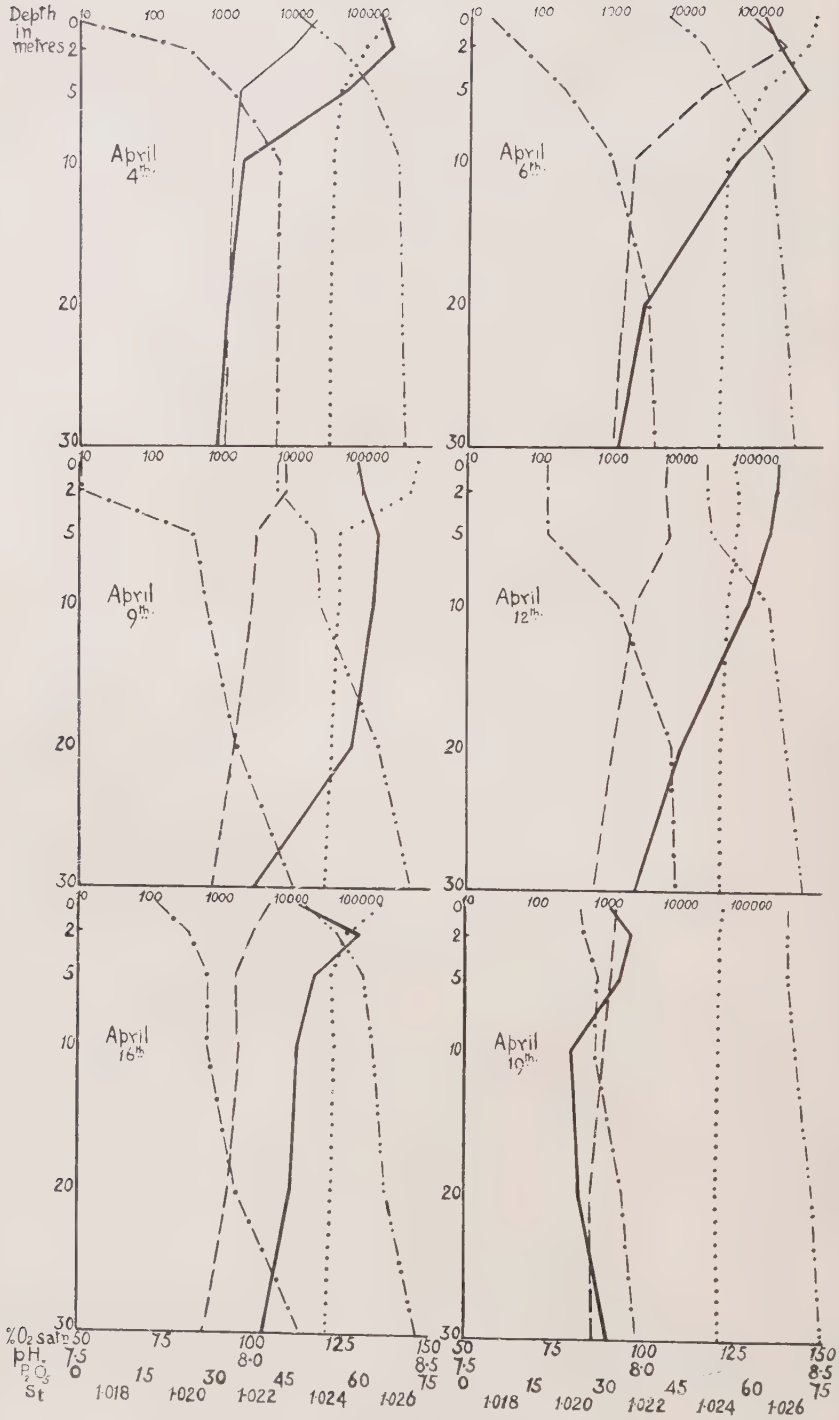

FIG. 5.—The spring increase in 1928 (contd.).

——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — .. — .. S_t.

maximum (138% at 2 metres), pH value had risen to 8·47, and phosphate had fallen at 2 and 5 metres. There are slight discrepancies in the phosphate results at surface and 2 metres on the 4th, 6th and 9th. These are due in part at least to the increased difficulty in matching colours when diatoms are very numerous.

It is curious that on the 6th, although the diatom present was as before, *Skeletonema costatum*, the type of cell was quite different from that of previous days, the cells being both larger and longer. This new type was found at surface and 2 metres while in all other samples they

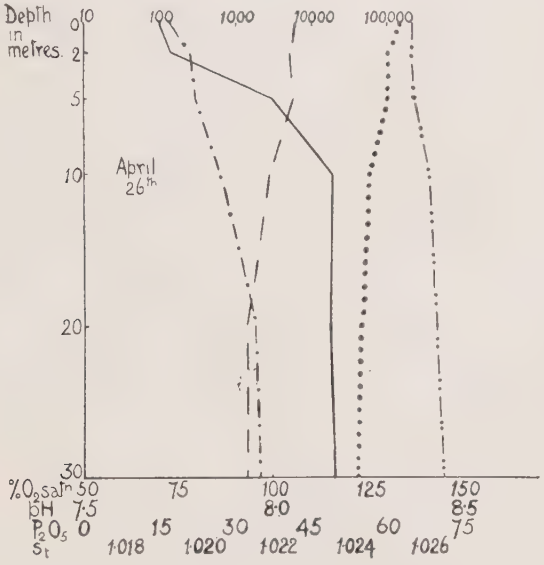

Fig. 6.—The spring increase in 1928 (contd.).
——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — .. — .. S_t.

were of the usual form. On April 9th the diatoms were sinking and numbers had fallen except in the deeper water. The new type of Skeletonema cell was predominant at surface and 2 metres, at 5 metres the types were mixed and below this a few chains of the new type were present at each depth. Density conditions had altered again, so that there was vertical mixing between 0 and 2 metres, and between 5 and 10 metres. The chemical factors were correspondingly altered. By April 12th mixing had gone on to 5 metres and had brought up a fresh supply of phosphate into the surface water, at the same time lowering pH and oxygen saturation values. With the introduction of phosphate the diatoms had increased slightly again at the surface and 2 metres.

The new type of cell had disappeared and all samples contained only the old type.

By April 16th the loch was stable once more and the diatoms were sinking, their numbers having decreased again except in deeper water.

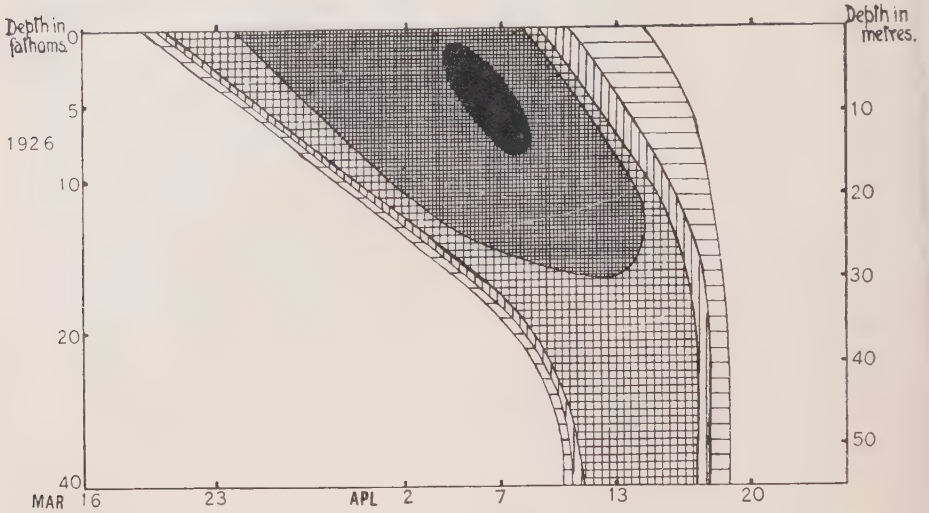

Fig. 7.—Diatom diagram. Spring increase of 1926.
□ under 50, ▭ 50–125, ▥ 125–250, ▦ 250–500,
▩ 500–1250, ■ over 1250 diatom chains per c.c.

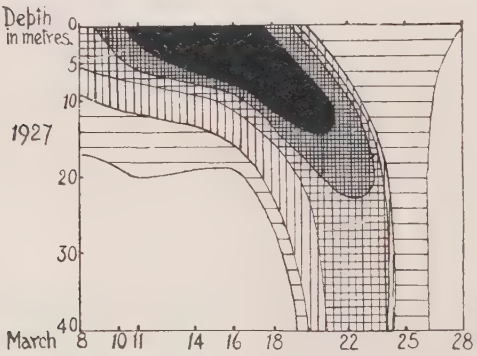

Fig. 8.—Diatom diagram. Spring increase of 1927.
□ under 50, ▭ 50–125, ▥ 125–250, ▦ 250–500,
▩ 500–1250, ■ over 1250 diatom chains per c.c.

There was still a fair amount of phosphate in the surface layers and it is difficult to understand why the diatoms stopped increasing at the surface. Diatom numbers were very low at all depths on the 19th and the distribution was irregular. The density gradient was only slight from top to

bottom and the loch appeared to be mixed. A week later it was visited again and there was evidence that another small increase of diatoms had taken place meanwhile, for the phosphate value had fallen a little, the pH value and oxygen saturation had risen and the diatoms increased in numbers down to 10 metres and then remained constant down to 30 metres.

The spring increase of 1928 was thus of a quite different type from that of 1926 and 1927, being much less regular. It began while vertical

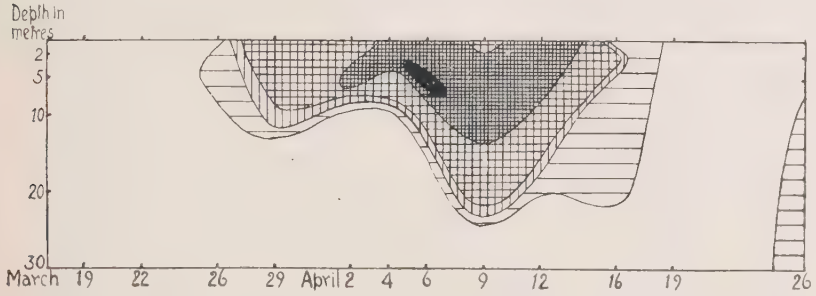

FIG 9.—Diatom diagram. Spring increase of 1928.
□ under 500, ▤ 500–1250, ||| 1250–2500,
▦ 2500–5000, ▩ 5000–12,500, ■ over 12,500 diatom cells per c.c.
The scales have been adjusted so that Figures 7, 8 and 9 are directly comparable.

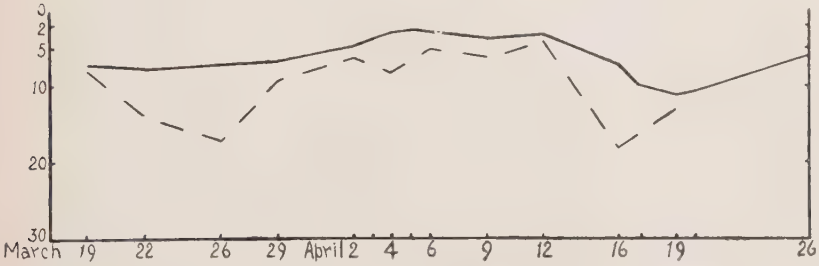

FIG. 10.—Secchi disc readings ———, and compensation-points for diatom cultures — — —, during the spring increase of 1928.

mixing was still going on and the diatoms increased in numbers simultaneously down to a considerable depth instead of only at the surface as usual. Since in deeper water there was not enough light for growth, the diatoms there sank as soon as mixing stopped and there was a great fluctuation in numbers at depths of 10 and 20 metres. When the temperature rose and stabilisation took place, the increase progressed much as in previous years, increasing rapidly at the surface and then sinking downwards. This process was interrupted, however, by further mixing, this time due to wind as well as temperature, and diatom numbers rose at the surface once more.

There are thus two factors responsible for the vertical distribution of the diatoms. First, there is the sinking of the diatoms which is strongly marked in the years 1926 and 1927 and is particularly clear in the late autumn of 1926 (Marshall and Orr, 1927). Second, there is the mixing of the diatoms which occurs when the sea-water itself is mixed by wind or temperature. This is recognisable by a uniform density at the depths mixed. This second factor was of considerable importance in 1928, but was found only on one occasion in 1927 (see p. 855). Another unusual event in the increase of 1928 was the change of diatom type for a short period, although the species remained unaltered. There was no apparent cause for either its arrival or its departure. Finally, as in the years 1926 and 1927, the end of the spring increase was not marked by a total lack of phosphate in the surface layers, but there was sufficient still in solution to supply another increase which in all probability followed after a short interval.

The spring increase starts at a time of year when the light for photosynthesis is comparatively poor, except at the surface, and the enormous number of diatoms present must decrease the light available still further. The figures for oxygen content are to some extent a measure of the amount of photosynthesis going on, but they are not reliable, partly because during the increase the water was often supersaturated and so gave too low an estimate of the oxygen produced, and partly because during the windy weather there was probably a good deal of movement among the different water layers. It was therefore thought of interest to estimate the amount of photosynthesis possible by sinking diatom cultures to different depths in the sea and measuring the amount of oxygen produced. Since the sea at that time was an almost pure culture of *Skeletonema costatum*, some samples of sea-water were tested in the same way. A culture of *Coscinosira polychorda* was used, while the sea-water samples used were taken from various depths (see Marshall and Orr, 1928). The most important external factor was, as might be expected, the number of diatoms present in the sea, and during the increase the total photosynthesis decreased from day to day as the cloud of diatoms in the water grew denser. Figure 11 and Tables 4 and 5 show two curves for diatom culture photosynthesis in the sea, the first taken before and the second during the spring increase of 1928. In the curve for March 22nd–23rd the oxygen production at 5 metres was considerable and the compensation-point lay between 10 and 20 metres. In the curve for April 6th–7th a steep fall occurred between $\frac{1}{2}$ and 2 metres and another between 2 and 5 metres, while the compensation-point lay between 2 and 5 metres. Since there was more sunshine on April 6th than on March 22nd, the smaller amount of photosynthesis going on at and below 2 metres must be ascribed to the effect of a thick screen of diatoms

in the surface water. The same type of result is seen in Figure 12 of which the curve for March 18th–19th was taken during, and that for March 28th–29th after the spring increase of 1927. After the diatoms had disappeared the photosynthesis at 5 metres increased again considerably. There was more sunshine on March 28th–29th than on March 18th–19th and the

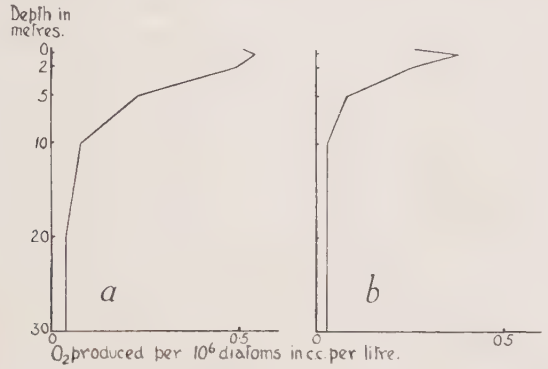

FIG. 11.—Oxygen production per 10^6 diatoms in Loch Striven, (*a*) 22–23/3/28 (0·41 hours sunshine), (*b*) 6–7/4/28 (4·25 hours sunshine).

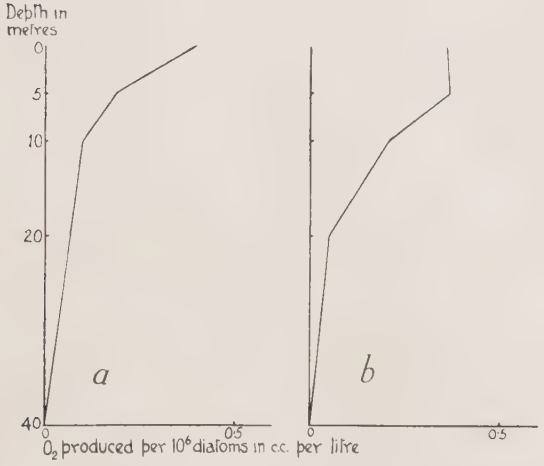

FIG. 12.—Oxygen production per 10^6 diatoms in Loch Striven, (*a*) 18–19/3/27 (no sunshine), (*b*) 28–29/3/27 (5 hours 50 minutes sunshine).

greater amount of photosynthesis at 5 metres may be due in part to this, but, as shown below, it is probable that it was also caused partly by the disappearance of the diatoms from the surface waters.

There is thus a relation between the type of curve and the number of diatoms present in the water. This is shown clearly in Figure 10 and Table 3,

where the compensation-points of eleven culture experiments carried out during the increase are plotted under the diatom increase diagram. The actual figures for compensation-points were arrived at by interpolation and are therefore only approximate. Before the increase began it was as deep as 17 metres, during the increase it rose as near the surface as 4 metres, and after the increase it sank again to 18 metres. This result is further confirmed by the Secchi disc readings which are plotted on the same figure. Before the increase the disc was seen to 7 metres and it disappeared at $2\frac{1}{2}$ metres during the height of the increase on April 5th. Diatoms were not counted on this day, but were at their recorded maximum on the 6th when the Secchi disc disappeared at 3 metres. After the increase was over, the reading was as deep as 11 metres. Confirmatory results were obtained with compensation-point figures in 1927, but Secchi disc readings were not taken. If allowance is made for the fact that the Secchi disc is not always seen as deep as the richest layer of diatoms, the correspondence becomes still more marked.

Poole and Atkins (1929) have found evidence of a decrease in the intensity of illumination due to the zoo-plankton, but did not find any effect produced by a diatom increase. While no data concerning the effect of the zoo-plankton are available for Loch Striven, the evidence quoted above seems to us conclusive concerning the obscuring effect of the phytoplankton. The results are not explicable either by rainfall or wind, the former by carrying down land detritus and the latter by agitation of the water. The much greater abundance of diatoms in the loch as compared with the open sea offers the most probable explanation of the discrepancy. The diatoms gave a distinct brownish tinge in columns of sea-water 15 cm. deep at the height of the increase and the quantity of detritus in centrifuged water samples was insignificant in comparison with the diatoms.

The experiments done with samples of sea-water taken during the course of the increase gave small and irregular results. The production was usually much less than that of a diatom culture and was often within, or very near to, experimental error. This is largely because the diatoms are so much smaller than the culture diatoms that twenty-four hours is hardly long enough to show production. Gaarder and Gran (1927) left samples of sea-water in flasks in the sea for periods of three days and got a considerable amount of oxygen produced. In our experiments the compensation-point was always found nearer the surface than in the case of culture diatoms. On an average the compensation-point for diatom cultures during the increase (7 experiments) was 8 metres, while that for sea-water experiments giving positive results (13 experiments) on the same dates as the above culture experiments was 3 metres. Since the sea diatoms do not produce so much as culture diatoms, it might be thought

that the illumination before the spring increase, although good enough for the latter (see Fig. 11a), was not good enough for the former to multiply. Proof that there is, at the surface at any rate, sufficient light for the growth of sea diatoms, was obtained in another way. Some weeks before the spring increase in 1928, a sample of sea-water was taken into the laboratory, filtered through a sterile sintered glass filter (see p. 868) and allowed to stand in an unheated room. After some days a good mixed culture of Skeletonema, Thalassiosira, Nitzschia and a few other small forms appeared. Similar results were obtained in December 1929 with both

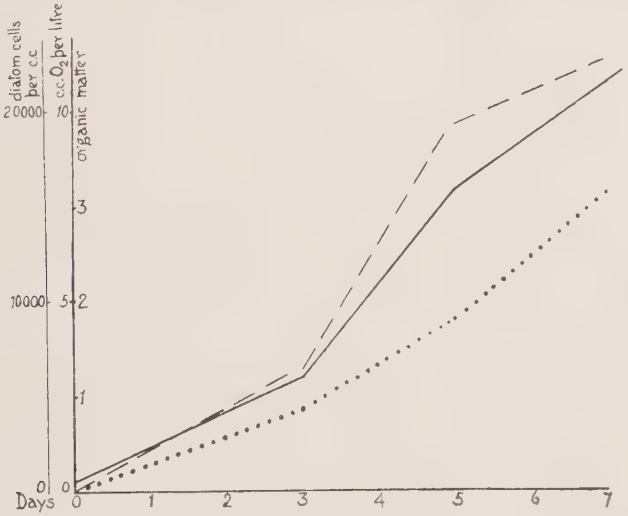

FIG. 13.—Curves showing relationship between ——— diatom numbers, — — — oxygen production, ... organic matter oxidisable by permanganate in a diatom culture in mg.O_2 per litre.

filtered and unfiltered water. It is apparent then that the sea diatoms themselves, as well as cultures, can grow in the ordinary illumination of the surface water before the date of the spring increase.

In view of the enormous production of diatoms during the spring increase, an attempt was made in 1928 to test whether there was a relationship between the organic matter oxidisable by permanganate in the sea (Ruppin, 1904) and diatom numbers. Because of the time required to complete the other work, the analyses for organic matter were not completed till two or three days after taking the samples. A disturbing factor is the inflow of water comparatively rich in dissolved organic matter from a burn at the head of the loch. This source of error was partially avoided by estimating the difference in organic matter between filtered and unfiltered samples. The filter used was a Jena sintered glass filter which

was found to be sufficiently fine in grain to stop practically all diatoms, although a few small forms were usually found on centrifuging the filtrate. The results were small but showed generally an increase with increasing diatom content. There was no good evidence that the organic matter in the filtered samples increased when the diatoms became richer, as would have been expected from the results obtained by Pütter (1924). He states that a large part of the organic matter produced by diatoms diffuses directly into the sea. Support was given to this work of Pütter's by Gran and Gaarder (1927), Gran and Ruud (1926), and Föyn and Gran

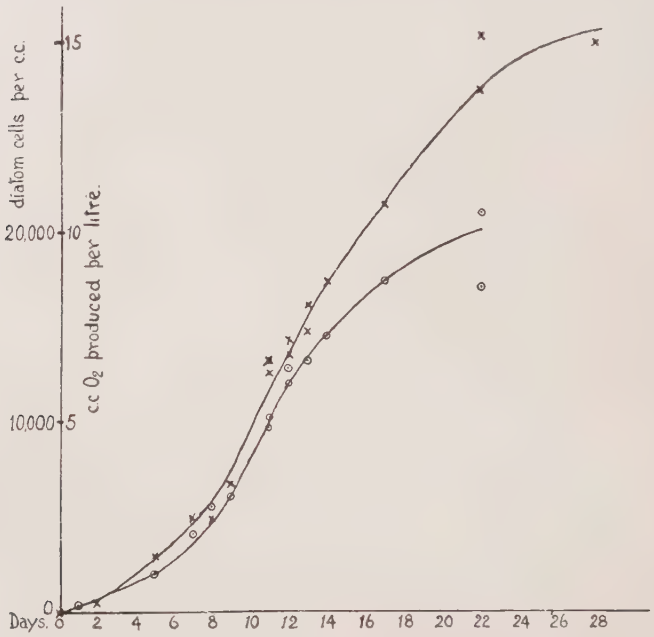

FIG. 14.—Diatom numbers (o) and oxygen production (x) in a diatom culture.

(1928) from results obtained in the Oslo fiord and later in the open sea. They used a biological method of estimating organic matter.

Since the results in sea-water are liable to error, some experiments were carried out with diatom culture, *Coscinosira polychorda* again being used. A few preliminary tests showed that while the total oxidisable organic matter was variable, the dissolved organic matter was higher in cultures old enough to have a fair number of dead cells. A culture was then started off by inoculating several litres of Miquel with a considerable amount of rich culture so that there were about 500 cells per c.c. This was then transferred to a large number of sterile stoppered bottles of about 120 c.c. capacity of which three were used for estimation of dissolved

oxygen content, diatom numbers and dissolved organic matter, filtered and unfiltered. The results obtained are shown in Figure 13 and Table 6. The difference in organic matter in the filtrate is negligible, showing that the dissolved organic matter does not increase along with the growth of diatoms but probably only when a number of the cells have died. The organic matter in the whole culture increases with the diatoms. At the end of the experiment the diatoms were very rich (21,300 cells per c.c.), so that, had diffusion of the organic matter taken place, the filtrate would have shown this clearly. Alkaline permanganate will, of course, only oxidise a portion of the organic matter present. In addition, though the analyses were made as described by Ruppin, it was found that, with diatom cultures, if the time of heating was increased the oxidation was also increased. It seems improbable, however, that any organic matter diffusing from the diatoms and so present in the filtered culture should have been entirely unaffected by it. While the above is true of a young culture, an old culture does show an increase in soluble organic matter, but this is more probably because the dead cells which are present are being attacked by bacteria.

The dissolved oxygen was estimated in the hope that it might be possible to find a factor by which the organic matter oxidisable by permanganate must be multiplied to give total organic matter. The increase of oxygen was so rapid and the degree of supersaturation so high that such a figure would be of doubtful significance. By the end of the experiment all the bottles had developed bubbles. The same type of growth was found in a similar experiment (Fig. 14) in which the slower rate of growth was probably due to the smaller amount of light in February than in May.

Discussion.

Of the many factors which might influence the beginning of the spring increase, there are several which can be excluded at once. The nutrient salts are probably present in abundance. Only one of these, phosphate, was actually estimated, but it does not seem likely that the mixing which led to the presence of phosphate did not bring up the other food salts also. Temperature also affects the spring increase only indirectly, since we find that on several occasions it started before the spring temperature overturn took place. We know, too, that Skeletonema can, and does, grow in waters both considerably warmer and considerably colder. It flourished at a temperature of 2–3° C. on the Norwegian coast in 1922 (Föyn, 1929), and at a temperature of 8–9° C. in Loch Striven in May, 1926 (Marshall and Orr, 1927), while it appears occasionally in the tropics (Karsten, 1907).

When we come to the question of light intensity the facts are more

complex. Diatom cultures grow well in winter, not only in the laboratory but also in the sea. The rate of growth is, of course, much slower than in summer and the growth in the sea shows that at the surface this effect is due chiefly to the shorter day. Below the surface the light intensity is suboptimal and growth is affected by both these factors. The result is that the compensation-point rises closer to the surface than in summer, to a depth of about 4 to 6 metres at midwinter (Marshall and Orr, 1928).

If we consider now the conditions for the sea diatoms themselves, we see that there is not only a sufficiency of food salts present in the sea throughout the winter, but the diatoms can grow in sea-water some time before the date of the spring increase if they are kept in a light approximately equal to that at the surface (see p. 867). Small diatom increases have been recorded after the autumnal temperature overturn has taken place. For example, in Loch Striven in November, 1926, there was a small increase of Skeletonema, and Atkins (1927*a*) has recorded an increase of Rhizosolenia in late autumn 1925 at Plymouth. In these cases food salts were present in sufficient quantity to have caused quite a large increase but did not do so. A probable explanation of this seems to be that the diatoms did not remain long enough in a sufficiently well-illuminated zone. In other words, the vertical mixing which takes place probably carries the diatoms below their compensation-point. Since the compensation-point in winter lies at 4 to 6 metres for culture diatoms and even nearer the surface for sea diatoms, it would need only a small vertical movement to bring the diatoms below their compensation-point. Such movements do occur in Loch Striven even in summer when the water is comparatively stable if there is a hard up-loch or down-loch wind and will be frequent in winter, during which time the loch is unstable. With the increasing light of the advancing spring, the compensation-point goes deeper and finally the diatoms will no longer be carried below it. Even after the increase has started, however, further mixing may modify its course considerably.

Gran (1929) has shown that on the Norwegian coast the spring increase near land is independent of the increase which occurs off the continental shelf. The former comes earlier and depends on the date of the melting of the snows. This fresh water lowers the salinity and adds large quantities of nutrient salts. In the Gulf of Maine also Bigelow (1924) believes that the spring increase depends on the nutrient salts added by the melting snows. This explanation will not hold for any area which has not a permanent covering of snow in winter, for the salts brought down by land drainage are being added all through the winter and are not held up to be added in a comparatively short time during the spring thaw.

On the other hand, Atkins (1928), among others, considers that the most important factor is the amount of spring sunshine. Figure 15 shows

the amount of sunshine daily during the spring months 1924–29, along with the date on which the number of diatom chains reached 20 per c.c. (or 200 in the case of diatom cells).* This is, of course, a purely arbitrary figure, but since the numbers usually increase very rapidly within a few days, the actual figure chosen makes little difference. It will be seen that the date of the spring increase is approximately constant, on about March 20th. In 1924 it was a little later and in 1927 a little earlier than usual, and it is interesting to notice that off the Norwegian coast in 1927

Fig. 15.—Daily sunshine during spring months of 1924–1929. The arrows show the beginning of the spring diatom increase.

it began exceptionally early too (Föyn, 1929). This was not a year with much early sunshine. At Plymouth the spring increase began earlier in 1924 than in 1925 (Atkins, 1927*b*), whereas the reverse was the case in the Clyde.

In Loch Striven, then, it appears that the date of the spring increase is decided chiefly by the total light which depends both on length of day and brightness. Only such a comparatively constant external factor could account for the narrow limits of time within which the increase

* The observations on diatoms in 1929 were made by Mr. Elmhirst.

begins. Vertical mixing may alter this date a little, but the increasing light gradually overcomes this factor and allows the spring increase to begin. As soon as the loch becomes stabilised the increase runs its normal course.

SUMMARY AND CONCLUSIONS.

1. The spring increase in Loch Striven is described in detail for three consecutive years. Contemporaneous experiments with diatom cultures and sea-water samples helped to elucidate the changes which occurred. Vertical mixing of the water layers was found to have an important effect on the form of the increase.

2. Although there is a relationship between organic matter oxidisable by permanganate and the total number of diatoms present, there is no relationship between *dissolved* organic matter oxidisable by permanganate and diatoms.

We wish to thank Mr. Elmhirst and members of the staff for their help throughout the work.

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TABLE 1.

1927.

Depth in m.	Temperature °C.	Salinity ‰.	Density.	Oxygen c.c. per l.	O_2 Saturation .	pH.	P_2O_5 mg. per c.m.	Diatom chains in 20 c.c.
8–3–27.								
0	6·79	31·97	1·0251			8·13	45	6,400
5	6·87	32·11	1·0253			8·12	50	5,400
10	7·18	32·30	1·0253			8·13	55	2,280
20	7·30	34·01	1·0262			8·14	59	423
40	7·38	34·43	1·0269			8·13	70	12
10–3–27.								
0	7·09	31·54	1·0247	7·60	109·6	8·18	38	16,700
5	7·22	33·02	1·0258	6·72	99·5	8·16	50	6,900
10	7·21	33·39	1·0262	6·33	98·4	8·14	52	2,800
20	7·30	33·78	1·0265	5·97	97·4	8·17	59	670
40	7·39	34·49	1·0270	5·85	97·1	8·13	58	65
11–3–27.								
0	7·11	32·41	1·0254	8·35	120·7	8·22	22	33,100
5	7·25	33·09	1·0259	7·16	104·2	8·14	36	16,400
10	7·21	33·39	1·0262	6·33	92·1	8·13	58	3,200
20	7·26	33·56	1·0263	6·12	89·5	8·12	69	1,050
40	7·29	34·39	1·0269	5·92	87·2	8·13	70	.....
14–3–27.								
0	6·27	30·21	1·0238	8·99	124·4	8·38	5	62,700
5	6·28	30·34	1·0239	8·98	125·2	8·37	13	51,000
10	7·22	33·30	1·0261	6·35	92·3	8·12	39	4,350
20	7·35	34·21	1·0268	5·89	85·9	8·12	52	402
40	7·38	34·39	1·0269	6·04	88·8	8·12	55	141
15–3–27.								
0	6·12	30·34	1·0239	8·96	124·5	8·36	20	
5	6·12	30·58	1·0241	8·92	123·9	8·35	17	
10	6·12	30·60	1·0241	8·88	123·3	8·35	22	
20	7·30	33·74	1·0264	5·82	85·2	8·12	66	
40	7·38	34·47	1·0270	5·88	86·7	8·10	72	
16–3–27.								
0	6·24	30·41	1·0239	9·18	127·6	8·46	10	47,500
5	7·17	30·55	1·0239	8·82	125·7	8·43	13	36,300
10	7·19	33·26	1·0260	6·23	90·6	8·21	47	6,300
20	7·28	33·82	1·0265	5·97	87·4	8·18	52	600
40	7·37	34·41	1·0269	5·81	85·6	8·18	64	138
17–3–27.								
0	6·18	30·33	1·0239	8·98	125·1	8·50	12	
5	6·14	30·31	1·0239	8·91	123·8	8·50	18	
10	7·19	33·73	1·0264	6·25	91·2	8·22	55	
20	7·13	33·88	1·0266	6·29	91·8	8·22	64	
40	7·38	34·46	1·0270	5·77	85·1	8·19	70	
18–3–27.								
0	6·49	30·07	1·0236	9·44	131·0	8·51	14	11,000
5	6·48	30·16	1·0237	7·91	110·6	8·35	20	39,600
10	7·11	33·30	1·0261	6·37	92·5	8·19	18	26,400
20	7·21	33·72	1·0264	6·17	90·1	8·19	63	2,740
40	7·35	34·48	1·0270	5·83	86·0	8·17	74	212

TABLE I (*continued*).

Depth in m.	Temperature °C.	Salinity ‰	Density.	Oxygen c.c. per l.	O Saturation %.	pH.	P_2O_5 mg. per c.m.	Diatom chains in 20 c.c
19–3–27.								
0	6·79	29·83	1·0234	9·00	127·0	8·49	12	
5	6·51	30·21	1·0237	9·07	126·9	8·47	14	
10	6·99	33·12	1·0260	6·66	96·5	8·21	35	
20	7·25	33·72	1·0264	6·00	88·1	8·17	57	
40	7·35	34·49	1·0270	5·87	86·6	8·18	62	
22–3–27.								
0	7·50	29·87	1·0233	7·75	110·7	8·48	13	1,280
5	7·53	30·05	1·0235	7·75	110·7	8·48	14	1,700
10	7·00	33·26	1·0261	6·61	95·7	8·23	31	16,100
20	6·92	33·24	1·0261	6·91	100·2	8·24	32	12,000
40	7·25	33·72	1·0264	5·91	86·4	8·19	68	7,400
23–3–27.								
0	7·57	28·79	1·0225	7·33	104·4	8·48	16	
5	7·47	31·92	1·0250	7·76	112·3	8·45	17	
10	7·12	32·99	1·0259	7·51	108·9	8·34	24	
20	7·17	33·70	1·0264	5·95	86·9	8·22	43	
40	7·33	34·41	1·0269	5·61	82·5	8·22	67	
25–3–27.								
0	7·20	31·24	1·0245	7·42	106·4	8·43	15	2,200
5	7·21	30·98	1·0243	7·42	105·9	8·42	19	1,700
10	7·20	31·24	1·0245	7.39	105·7	8·42	21	2,200
20	7·03	33·37	1·0262	6·40	92·6	8·26	51	2,300
40	7·32	34·26	1·0268	6·15	90·3	8·22	69	2,200
26–3–27.								
0	7·17	29·32	1·0230	7·38	104·2	8·41	18	1,090
5	7·20	31·97	1·0250	7·55	108·6	8·34	18	67
10	7·18	32·40	1·0254	7·51	108·3	8·34	23	143
20	7.02	33·14	1·0260	6·70	97·0	8·26	30	688
40	7·30	34·10	1·0267	5·36	78·6	8·16	63	192

TABLE 2.

1928.

Depth in m.	Temperature °C.	Salinity ‰	Density.	Oxygen c.c. per l.	O_2 Saturation %.	pH.	P_2O_5 mg. per c.m.	Diatom cells in 20 c.c.
14–3–28.								
0	5·56	32·66	1·0258	6·75	94·5	8·22	33	2,182
2	5·50	32·65	1·0258	6·75	94·1	8·22	34	2,246
5	5·50	32·65	1·0258	6·79	94·6	8·21	41	2,191
10	5·52	32·65	1·0258	6·76	94·3	8·21	35	2,607
20	6·24	33·02	1·0260	6·31	89·5	8·21	36	579
19–3–28.								
0	5·55	32·38	1·0255	6·95	96·9	8·23	32	8,100
2	5·51	32·38	1·0256	6·92	96·3	8·22	42	7,300
5	5·50	32·34	1·0255	6·90	96·0	8·22	38	7,300
10	5·50	32·38	1·0256	6·91	96·2	8·21	39	7,600
20	6·17	33·30	1·0262	....	....	8·21	40	1,900

TABLE 2 (*continued*).

Depth in m.	Temperature °C.	Salinity ‰	Density.	Oxygen c.c. per l	O_2 Saturation %.	pH.	P_2O_5 mg. per c.m.	Diatom cells in 20 c.c.
22–3–28.								
0	5·63	32·01	1·0253	6·91	96·2	8·21	32	7,600
2	5·50	32·01	1·0253	6·90	95·7	8·19	34	8,300
5	5·58	31·87	1·0252	6·95	96·5	8·21	33	8,800
10	5·67	32·25	1·0254	6·87	95·9	8·20	34	7,800
20	5·94	32·89	1·0259	6·77	95·4	8·19	37	6,800
30	5·99	33·04	1·0260	6·78	95·9	8·20	38	3,400
26–3–28.								
0	5·93	31·85	1·0251	6·85	95·7	8·22	33	9,000
2	5·97	31·75	1·0250	6·92	97·0	8·21	36	11,300
5	5·85	31·87	1·0251	6·93	96·8	8·21	37	13,500
10	5·90	32·83	1·0259	6·64	93·5	8·20	35	2,900
20	6·02	33·15	1·0261	6·55	92·8	8·19	38	1,800
30	6·19	33·49	1·0264	6·37	90·7	8·21	40	1,500
29–3–28.								
0	5·95	31·52	1·0248	6·95	97·2	8·22	30	64,000
2	5·95	31·70	1·0250	7·01	98·1	8·22	30	68,000
5	5·97	31·75	1·0250	7·00	98·0	8·20	31	57,000
10	5·95	32·21	1·0254	6·83	96·0	8·20	33	41,000
20	6·02	33·02	1·0260	6·57	93·0	8·20	37	2,000
30	6·09	33·27	1·0262	6·42	91·2	8·20	40	1,050
2–4–28.								
0	6·62	30·36	1·0239	7·43	104·2	8·25	23	73,000
2	6·50	30·44	1·0239	7·53	105·6	8·24	24	61,000
5	6·09	31·62	1·0249	7·32	102·7	8·25	26	133,000
10	6·08	32·63	1·0257	6·65	93·9	8·22	34	8,000
20	6·22	33·34	1·0262	6·25	89·0	8·20	41	1,200
30	6·36	33·68	1·0265	6·18	88·4	8·20	42	115
4–4–28.								
0	6·55	29·54	1·0232	8·37	117·1	8·37	0	180,000
2	6·48	30·98	1·0243	7·79	109·7	8·31	22	248,000
5	6·18	31·99	1·0252	6·73	94·8	8·24	32	60,000
10	6·12	33·02	1·0260	6·56	93·1	8·22	42	2,100
20	6·12	33·15	1·0261	6·53	92·7	8·21	42	1,250
30	6·15	33·25	1·0262	6·37	90·6	8·21	42	890
6–4–28.								
0	6·49	28·56	1·0225	9·33	129·2	8·47	5	128,000
2	6·96	29·93	1·0235	9·77	138·0	8·44	10	199,000
5	6·56	30·76	1·0242	8·28	116·6	8·32	19	510,000
10	6·19	32·24	1·0254	6·81	96·1	8·22	30	56,000
20	6·11	32·81	1·0258	6·55	92·8	8·21	37	3,100
30	6·11	33·19	1·0261	6·41	91·2	8·20	39	1,280
9–4–28.								
0	7·00	28·83	1·0226	7·77	109·0	8·46	0	90,000
2	7·00	28·81	1·0226	7.76	108·8	8·44	0	106,000
5	6·77	30·21	1·0237	7·05	99·5	8·24	24	176,000
10	6·73	30·27	1·0238	7·04	99·1	8·24	27	152,000
20	6·27	32·45	1·0255	6·60	93·6	8·22	34	77,000
30	6·28	33·54	1·0264	6·15	88·0	8·20	46	3,500
12–4–28.								
0	7·15	30·32	1·0237	7·47	106·3	8·24	17	225,000
2	7·14	30·21	1·0237	7·47	106·0	8·26	17	220,000
5	7·13	30·32	1·0238	7·51	106·7	8·25	17	169,000
10	6·40	32·31	1·0254	6·83	96·8	8·23	32	83,000
20	6·17	32·89	1·0259	6·43	91·2	8·21	43	10,000
30	6·30	33·55	1·0264	6·04	86·3	8·21	44	2,400

TABLE 2 (*continued*).

Depth in m.	Temperature °C.	Salinity ‰	Density.	Oxygen c.c. per l.	O_2 Saturation %.	pH.	P_2O_5 mg. per c.m.	Diatom cells in 20 c.c.
16–4–28.								
0	7·20	29·88	1·0234	7·43	105·4	8·36	17	14,200
2	6·70	30·97	1·0243	7·06	99·7	8·26	24	99,000
5	6·50	31·97	1·0251	6·71	95·1	8·22	28	24,000
10	6·50	32·30	1·0254	6·72	95·6	8·23	28	13,800
20	6·36	32·72	1·0257	6·57	93·4	8·22	34	10,900
30	6·26	33·76	1·0266	6·00	85·8	8·21	48	4,700
19–4–28.								
0	6·32	33·03	1·0260	6·47	92·1	8·22	24	1,120
2	6·32	33·09	1·0260	6·45	91·9	8·21	25	2,015
5	6·29	33·09	1·0260	6·41	91·3	8·21	28	1,400
10	6·29	33·27	1·0262	6·25	89·0	8·21	28	306
20	6·40	33·94	1·0267	5·90	84·7	8·20	33	400
30	6·40	34·20	1·0269	6·06	87·1	8·21	36	1,008
26–4–28.								
0	7·52	32·74	1·0256	7·19	104·7	8·33	17	101
2	7·43	32·77	1·0256	7·18	104·4	8·30	21	138
5	7·18	32·77	1·0257	7·22	104·6	8·30	22	3,072
10	6·67	33·30	1·0261	6·88	98·8	8·25	27	18,400
20	6·50	33·47	1·0263	6·50	93·1	8·23	34	17,800
30	6·47	33·65	1·0265	6·47	92·7	8·22	35	19,600

TABLE 3.

Date	March 19	22	26	29	April 2	3	4	5	6	9	12	16	17	19	20
Compensation-point of culture in metres.	8	14	17	9	6	–	8	–	5	6	4	18	—	13	—
Secchi disc reading in metres.	7	7½	—	6½	4½	3½	2¾	2½	2¾	3½	3	7	9½	11	10½

TABLE 4.

Loch Striven. 22–23/3/28. 0·41 hours sunshine.
Diatom culture of Feb. 20th—7,400 cells per c.c.
12.20 p.m.–11.45 a.m. Initial O_2 content 1. 8·21, 2. 8·18, 3. 8·22 } 8·20

Depth in metres.	Light.		Dark.	Av.	Total O_2 produced.	O_2 produced by 10^6 diatoms.
0	11·26, 11·65	11·46	7·70	7·73	3·74	0·51
½	11·64, 11·88	11·76	7·75	7·73	4·03	0·54
2	11·34, 11·41	11·38	7·74	7·73	3·65	0·49
5	9·51, 9·55	9·53	7·71	7·73	1·80	0·23
10	8·37, 8·29	8·33	—	7·73	0·60	0·08
20	8·01, 8·04	8·02	7·79	7·73	0·29	0·04
30	7·95, 8·03	7·99	7·68	7·73	0·26	0·04

TABLE 5.

Loch Striven. 6–7/4/28. 4·25 hours sunshine.
Diatom culture of March 7th—8,300 cells per c.c.
11.35 a.m.–11.15 a.m. Initial O_2 content $\left.\begin{matrix}7{\cdot}71\\7{\cdot}72\end{matrix}\right\}$ 7·72

Depth in metres.	Light.		Dark.	Av.	Total O_2 produced.	O_2 produced by 10^6 diatoms.
0	9·11 9·04	9·08	6·86	6·89	2·19	0·26
½	10·21 9·84	10·02	6·92	6·89	3·13	0·38
2	8·98 9·01	8·99	Lost	6·89	2·10	0·25
5	7·56	7·56	6·86	6·89	0·67	0·08
10	7·15	7·15	6·91	6·89	0·26	0·03
20	Lost		6·94	6·89	——	——
30	7·10 7·14	7·12	Lost	6·89	0·23	0·03

TABLE 6.

Date.	Diatom cells per c.c.	Oxygen c.c. per litre.	Oxygen produced.	Oxidisable Organic Matter. Total mg. O_2 per litre.	Production mg. O_2 per litre.	In filtered samples mg. O_2 per l.
4–5–28	575	5·89	0	1·36	0	1·24
7–5–28	6,000	9·07	3·18	2·22	0·86	—
9–5–28	15,700	15.48	9·59	3·15	1·79	—
11–5–28	21,300	17·13	11·24	4·46	3·10	1·22

Bacteria of the Clyde Sea Area: A Quantitative Investigation.

By

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With 7 Figures in the Text.

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Introduction.

The importance of bacterial action in the seas has long been recognised, but investigation in marine bacteriology lags behind that of corresponding terrestrial problems. Such general information about marine bacteria as is now available is derived mainly from bacteriological work of some decades ago. At that time the technique of the science was not fully developed, but at the present day it has become so specialised that it lies outside the province of the marine biologist, although he alone is able to appreciate the significance of bacteria in the general economy of the sea.

Whilst the part played by bacteria in the food-cycle of the sea depends partly upon special features in the metabolism of the various bacterial species, it obviously depends chiefly upon the abundance of such organisms. Now in an investigation of the numbers of bacteria in any sample, it is extremely important that due regard be paid to the conditions under which the work is performed. In much of the early work on marine bacteria the experimental methods are not described. Where such

information is available, one finds that there is lack of uniformity in the experimental methods adopted, and that therefore the results of different workers are not readily comparable with one another. Standard routine methods are needed for the bacteriological examination of sea-water, such as are customary for the routine analysis of fresh water. It is significant that among the various bacteriological handbooks on the technique of water-examination, none that has come to the writer's notice gives consideration to the special aspects of marine bacteriology.

It is the purpose of this paper to present a quantitative report on the marine bacteria of the Clyde Sea Area. This report is based on observations carried out over a period of 18 months, standardised routine methods having been devised for taking the samples and for laboratory technique.

Historical.

The earliest numerical record of marine bacteria appears to be that of Sanfelice (see Bertel, **5**), who found in 1889 that the number of organisms in the sea decreased as the distance from the shore increased. From this he deduced that bacteria in the sea were not native to it, but terrigenous, "apportées à la mer avec les ordures." This prompted de Giaxa (**11**) to investigate the viability of pathogenic organisms in sea-water. He found that they flourished in sterile sea-water but did not survive competition with other forms in unsterilised sea-water—a finding that has been confirmed in more recent years by the Royal Sewage Commission (**16**). Russel (**21**), who analysed samples from the Gulf of Naples and the Atlantic, observed that the number of bacteria decreased from the surface down to 200 metres; he also noted that marine mud contained many more bacteria than the water immediately above. Schmidt-Nielsen (**23**), however, found the reverse to hold, obtaining for northern waters an average of 26 bacteria per c.c. at the surface and 420 per c.c. at 25 metres.

Fischer's report (**10**), which is based on samples taken by the German Plankton Expedition of 1889, is the most comprehensive account of marine bacteria. He gave full accounts of technique employed and furnished descriptive and statistical analyses of the water samples obtained. His results vary very much, but in general he found that there were fewer bacteria at greater depths than at the surface. He noted also that the numbers were greater at sunrise than in the afternoon.

The Prince of Monaco made some analyses of the Atlantic sea-water, and found the bacterial content to be extremely high between the Azores and Portugal (see Bertel, **5**); this he attributed to the existence of a submarine ridge with very rich fauna.

In 1911 Bertel (**5**) investigated the bacteria of the sea-water off Monaco,

and found (1) that the number of bacteria diminished progressively from coastal areas outwards, (2) that the number of bacteria increased from the surface downwards, and (3) that the number at the surface increased during the night, and diminished during the early hours of the morning.

Experimental Technique.

Sampling Stations.

Regular monthly samples were taken at three stations which were selected as likely to be different yet characteristic areas; in addition, samples were taken at less regular intervals at other places.

The regular stations were :—

1. *Loch Striven.* This loch is notably free from steamer traffic, and the adjoining land is sparsely populated. It thus represents an area remarkably free, in view of its proximity to land, from industrial or other human contamination.

2. *Loch Long* (*Thornbank Station*). This station is moderately free from land contamination, but there are habitations along the shores of the loch, and there is a certain amount of boat traffic. Terrestrial influences are thus more marked here than in Loch Striven.

3. *Greenock.* Here the water is estuarine in character, and highly polluted with sewage, with waste from sugar refineries and with industrial effluents generally, which are emptied into the River Clyde. This area was chosen in order to determine to what extent the true water bacteria would be outnumbered by those species present as a result of contamination. A detailed account of the Clyde Sea Area is given by Mill (**19**); a map of the area and a summary are also given by Marshall and Orr (**17**).

Sampling Technique.

Vertical series of samples were taken periodically at the above-mentioned stations. It was necessary to employ an apparatus capable of collecting water at the desired depth without taking in water from other depths when being hauled up. The closing water-bottles generally employed in marine work are not suitable for the collecting of sea-water destined for bacteriological analysis. The following are the principal objections : (i.) Such bottles are made of metal, and most metals have a marked bactericidal effect. This objection is not a cogent one if the sample is in the bottle for only a short time (**3**). (ii.) When a series of samples has to be taken with one bottle, each sample has to be siphoned into a sterile container for transport ashore, and while this operation is being carried out there is a risk of contamination. (iii.) Between the taking of successive samples it would be necessary to sterilise the bottle,

and these water-bottles are usually so unwieldy that it is laborious to accomplish this effectively.

Several bacteriological samplers have been described, notably those by Bertel (**4**), Russel (**21**), Portier and Richard (**20**), Drew (**8**, **9**), Matthews (**18**), Birge (**6**) and Sclavo-Czaplewski (**14**). The simplest type consists essentially of a stoppered bottle, the stopper being pulled out at the required depth. The chief disadvantage of the method is that the removal of the stopper requires a second line which is apt to foul the lowering wire. The second type consists of a glass container with a drawn-out sealed tip ; this tip can be broken by a messenger when the apparatus is at the required depth. Matthews has described a deep-sea bacteriological water-sampler of more complicated design than the foregoing.

For the work described in the following pages a comparatively simple apparatus was required, capable of use to a depth of 60 fathoms. Eventually a sampling apparatus similar to that described by Birge (**6**) and Wilson (**24**) was selected.

It consists of (i.) a glass sampling tube and (ii.) a metal tube-holder. The tube is an ordinary combustion tube 15 cm. $\times$ 3 cm., fitted with a one-holed rubber cork. Through this projects a glass tube bent at a right angle, having the end drawn out and sealed at about 12 cm. from the bend. The right-angle tubes are fitted into the corks, and together with the combustion tubes sterilised by steam. These are then fitted together, due precautions being taken to avoid contamination of the parts.

The tube-holder consists of a plate-sinker A (Fig. 1), with a spring clamp B to hold the sampling tube in position. At the top of the sinker is a projecting arm at the free end of which is a small brass breaking pin C. There is also a lever arm D so placed that when the sampling tube is in position the tip of the inlet tube lies immediately above the end of the lever arm and immediately under the breaking pin. When the apparatus reaches the required depth a messenger is sent down the connecting wire to operate the lever arm ; in this manner the tip of the capillary tube is broken.

The above apparatus was modified by Wilson from the sampler used by Russel (**21**) and was designed for limnological work in shallow waters down to 23 metres ; Wilson evacuated his sampling tubes, but the author found experimentally that at a depth of 10 fathoms a tube filled with air at atmospheric pressure would take a sample whose volume would be about half that of the whole tube ; at greater depths, the increased pressure caused proportionally greater filling of the tube. Most of the samples were taken at depths greater than this, and it was necessary to evacuate only those tubes destined to take surface samples.

The apparatus was sent down on a Kelvin sounding wire worked from a sounding machine recording in fathoms.

Evacuation of the surface sampling tubes was accomplished in the following manner: sterile glass tubing was prepared as shown in Figure 2 and attached to a sterile sampling tube. This was evacuated to a pressure

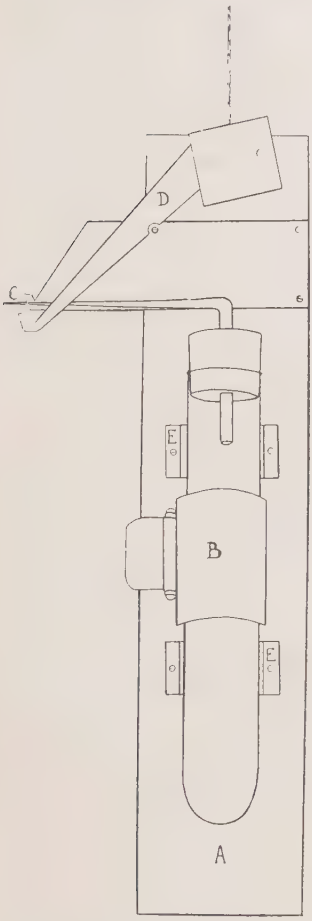

Fig. 1.—Wilson's bacteriological water-sampler, showing sampling tube in position and lever arm open. A, plate-sinker; B, spring clamp; C, breaking pin; D, lever arm; E, rubber cushion.

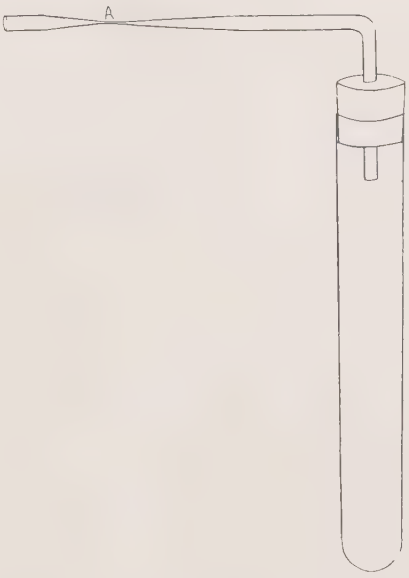

Fig. 2.—Surface sampling tube prepared for evacuation. The tube is attached to a filter pump, and sealed off at A.

of 30–60 mm. and sealed off at A. The connections at the rubber were made air-tight with paraffin wax.

The advantages of this apparatus lie chiefly in its simplicity, the extreme rapidity with which a series of samples can be taken at any one station, and the circumstance that the same tube serves both for taking the sample and for transporting it to the laboratory. The rubber cork is

liable to be forced inwards as the sampler descends; if this occurs the tube breaks at the right-angle bend. In practice this can be avoided by selecting well-tapered corks, though for constant deep-water work it would be necessary to have the sampling tube and the inlet arm blown in one piece after the retort-shaped type used by Drew (**8**) for depths greater than 70 fathoms.

While the sampler is being hauled up, the tip of the tube is of course open, but there is no admixture with water from the upper layers through which it is passing, for as the apparatus is being raised the pressure in the tube is being continuously reduced and the compressed air is flowing out of the tube at the narrow orifice. An inflow of water is therefore prevented.

For the quantitative work described below, samples were taken in vertical series at intervals of 10 fathoms from the surface downwards. For transit ashore the open tips of the tubes were sealed off in the flame of a spirit lamp, and packed in sterilised cotton-wool.

Transport of Samples.

In making total counts of the bacterial content of water the following are significant factors :—

(i.) The time interval which elapses between the taking of the sample and its examination in the laboratory, because during that period the bacteria present in the sample may be actively dividing. In the course of this work, the samples at any one station were always taken at the same time of day, and dealt with in the laboratory after approximately the same time interval. In this way uniformity of treatment was ensured, and the numerical results so obtained at any one station for different dates are comparable with one another.

	Time of Sampling.	Time of Inoculating.
Loch Striven	12.30 p.m.	5.0 p.m.
Loch Long	1.0 p.m.	5.30 p.m.
Greenock	4.0 p.m.	6.0 p.m.

(ii.) The temperature at which the samples are kept during transport. It is advisable to inhibit bacterial reproduction by keeping the samples on ice until they are examined in the laboratory. It was found that when samples were transported in a padded box, the temperature of the water on arrival at the laboratory was not raised more than 2° C.; the rate of multiplication of the bacteria would thus not be appreciably increased.

Laboratory Technique.

The technique adopted for routine work followed as nearly as possible the procedure recommended by the American Society of Bacteriologists

(1) for the standard examination of water. The regular bacteriological examination of sea-water does not appear to have called for special attention in their schedule.

The following culture media were used :—

Standard Agar.

Tap-Water	1000 gm.
Lab-Lemco	3 gm.
Peptone (Witte's)	10 gm.
Agar	15 gm.
NaCl	5 gm.

The medium was prepared in the usual way, cleared with 10 gm. egg-albumen dissolved in 100 c.c. of water, and adjusted with NaOH to neutral, using phenolphthalein as an indicator. The agar was sterilised by autoclaving for 30 minutes at a pressure of 2 atmospheres (Giltner, **12**, p. 40).

The following modifications were tried experimentally :—

(i.) Tap water and NaCl were replaced by filtered sea-water.
(ii.) NaCl was replaced by 34 grams of evaporated sea salt.
(iii.) Tap water and Lab-Lemco were replaced by fish extract. The fish extract was prepared by slowly heating 1 kilog. of cod in 1 litre of sea-water for about 4 hours ; it was then filtered and made up to 1 litre with tap water.

These media all favoured growth, but they were not found to be markedly superior to the ordinary bacteriological media, and therefore they were not used for routine quantitative work.

Standard Gelatine. This was prepared in the same manner as the foregoing, using 150 grams of gelatine per litre instead of the agar (**12**, p. 35).

Conradi-Drigalski Agar.

(*a*)	Water	2 litres.
	Agar	60 gm.
	NaCl	10 gm.
	Nutrose	20 gm.
	Peptone	20 gm.
	Lab-Lemco	6 gm.
(*b*)	Azolitmin (2·5%)	40 c.c.
	Lactose	30 gm. in 100 c.c. water.
	Na_2CO_3 (10%)	4 c.c.
	Crystal Violet (0·1 gm. in 100 c.c.)	20 c.c.

The agar (*a*) is prepared in the usual way and sterilised. The ingredients (*b*) are sterilised separately and added to the hot agar (**12**, p. 387).

On this medium the growth of non-intestinal organisms is inhibited. The presence of colonies is presumptive evidence of fæcal contamination; the coliform lactose-fermenting species appear as red colonies, and the typhoid-dysentery group as white or blue colonies.

McConkey Agar.

Water	500 c.c.
Peptone	10 gm.
Agar	7·5 gm.
Neutral Red (1%)	1·25 c.c.
Sodium taurocholate	2·5 gm.
Lactose	5 gm.

The lactose is added to the hot agar after filtration. This medium also inhibits the growth of non-intestinal species.

Litmus-lactose-bile-salt Broth.

Tap Water	1000 gm.
Sodium taurocholate	5 gm.
Peptone	20 gm.
Lactose	10 gm.
Azolitmin (2%)	20 c.c.

The peptone and sodium taurocholate are boiled and the lactose and azolitmin added afterwards. Fermentation of the lactose is presumptive evidence of the presence of intestinal organisms (**12**, p. 382).

Of the above media, the first two were used for ordinary quantitative work, and the last three for the detection of pollution.

Plate cultures were made by adding measured volumes of the sample to the nutrient media. The inoculations were made at as low a temperature as possible, i.e. above 35° C. for agar, and above 25° C. for gelatine. At this temperature the medium is still liquid, and is not so hot as to kill the ordinary micro-organisms.

From each water sample the following cultures were made :—

(*a*) Agar : 1·0 c.c., 1·0 c.c. (duplicate), 0·5 c.c., 0·1 c.c., and a control plate, not inoculated.

(*b*) Gelatine : as for agar.

(*c*) Conradi-Drigalski agar : 1·0 c.c.

(*d*) McConkey agar : 1·0 c.c.

(*e*) Litmus-lactose-bile-salt broth : one tube culture.

Quantitative Work. Cultures (*a*) and (*b*) were incubated in dark containers at room temperature. At the fifth day after inoculation the number of colonies was counted with the naked eye; after this period of incubation the number was fairly constant.

Some departures were made from the accepted routine for the bacteriological examination of water. Firstly, the incubation temperature was some six to twelve degrees lower than that usually employed. This was done for two reasons: (i.) to encourage the growth of the true water bacteria, which appear to thrive better at a temperature lower than that which favours soil bacteria; freshwater bacteria, and presumably marine bacteria also, are extremely sensitive to high temperatures both during plating and during incubation. (ii.) to discourage the growth of any organisms present which grow best at higher temperatures, as, for example, coliform bacteria. In this way the colonies which grew on the agar and the gelatine plates were representative chiefly of the true water bacteria.

A second departure from the usual routine was that the dilution method not being necessary was not employed. It had been ascertained by preliminary tests that the number of colonies obtained from an inoculum of 1·0 c.c. could easily be counted. In the Greenock area the total number of bacteria was very high, but this was due largely to putrefactive and intestinal organisms, and since their growth was discouraged by the low incubation temperature employed, the numbers obtained on agar and gelatine plates represent the approximate number of true water bacteria and not the total number of bacteria present.

A third point of difference from ordinary routine lay in the method of recording results. The American Society of Bacteriologists (1) recommend that, in order to avoid fictitious accuracy, the numbers obtained from bacterial counts should be approximated as under :—

1– 50 recorded as enumerated.
51– 100 recorded to the nearest 5.
101– 250 recorded to the nearest 10.
251– 500 recorded to the nearest 25.
501–1000 recorded to the nearest 50.

This recommended procedure is, however, intended for use in reports based on the evidence of one sample only for any one locality. This plan was not adopted in this work, but the actual figures obtained are given, since a number of plates was made for each sample and a number of samples was taken for each place at intervals throughout a year.

Detection of Pollution. Conradi-Drigalski and McConkey plates (*c*) and (*d*) and broth tube (*d*) were incubated at 37° C. for 24 hours. Any

colonies which appeared by the end of that period were presumptive coliform organisms, the red colonies being of course lactose fermenters. When the numbers so obtained were compared with the gelatine and agar counts for the same sample, it was possible to estimate the proportion of high-temperature intestinal organisms to low-temperature free-living organisms. This indicated not only whether the water sampled was polluted or not, but also the degree of pollution of the sample.

Results.

Loch Striven. This is the type area of natural sea-water, with minimal contamination despite its proximity to land. The numerical results of the plate cultures made from the samples taken each month are given in

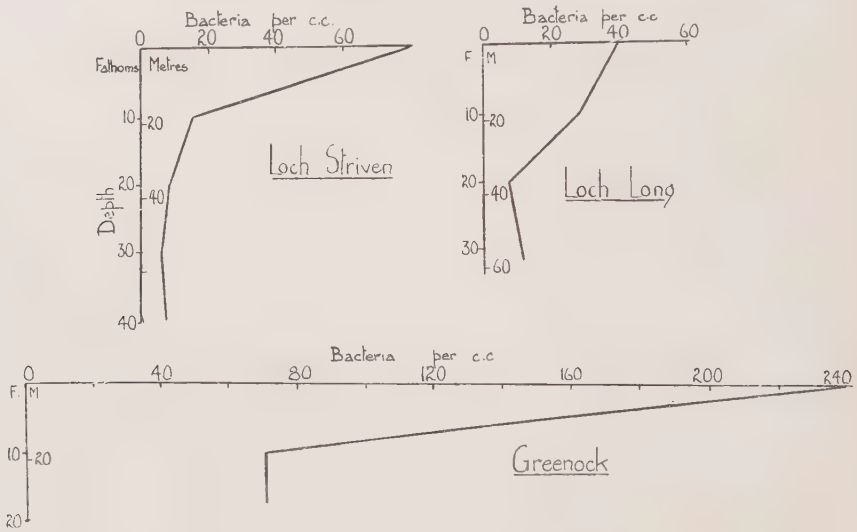

Fig. 3.—Average number of bacteria per c.c. for the year, May, 1928–April, 1929.

Table I. The average number of bacteria per c.c. is estimated for each sample from the total volume of water-sample plated out (usually 5·2 c.c.) ; these averages are given in the last column.

Samples were taken at the surface, and at intervals of 10 fathoms down to the bottom ; the bottom sample was taken immediately above the mud, in approximately the same place, but as the sides of the loch were steep, the depth at which the bottom sample was taken varied from 37 to 40 fathoms.

The following results are noted :—

Vertical Variation. 1. The number of bacteria per c.c. is low compared with that of other stations in the Clyde Sea Area.

2. The number of bacteria is greater at the surface than at lower levels (Fig. 3).

3. At the surface, the bacterial content of the water fluctuates much more than in deep waters, where it is more nearly constant.

4. At and below 10 fathoms, the number of micro-organisms does not exceed 30 per c.c. at any season.

5. Bottom samples show a rather lower bacterial content than the water at higher levels. This is an unusual feature, which will be discussed in the following section.

Seasonal Variation. 1. The numbers of bacteria per unit volume vary only little throughout the course of a year. Any variations outside the limits of accuracy of the experimental methods adopted appear to be erratic and therefore cannot be correlated with any factor varying seasonally. Such fluctuations may be due to external factors which operate only intermittently. This is particularly applicable to the surface waters, whose composition varies so much with conditions affecting drainage from the land (**17**).

2. At the surface and below, the bacterial content is relatively high in August.

Diurnal Variation. The samples just described were taken at intervals of several weeks, so they do not show short-period variations due to such factors as tide, sunshine, and perhaps diatom increases. Accordingly, samples were taken in vertical series quarterly at 3-hour intervals over a period of 24 hours. The experimental conditions differed from those under which the other periodical samples were examined. Plating was done on the boat immediately after sampling; two agar plates were made from each sample, using 1·0 c.c. as inoculum. Gelatine plates were not employed, as the lower solidifying point of gelatine made it unsuitable for plating work carried out on a boat. Four such 24-hour series were made. The results are given in Tables IIA, IIB, IIC and IID.

Winter Series, December 19/20, 1928. The following results were observed :—

1. The general vertical distribution over the 24 hours agrees with that of the monthly samples, i.e. there is a progressive decrease in the bacterial content from the surface to the bottom and the surface samples show wider fluctuations.

2. The number of surface bacteria is unusually high : this may be correlated with the fact that the herring fishing was in progress at the time.

3. At any given depth the numbers were higher at night, with a tendency to decrease from 7 p.m. till the early hours of the morning

(Fig. 4). With increasing depth the maximum occurs at a later hour, but this may be due to chance variations.

Spring Series, March 7/8, 1929. From Table IIB the following observations were made :—

1. The number of surface bacteria is unusually low. This may have been due to the low temperature then prevailing, and to the fact that the herring fishing had ceased some weeks earlier. These possible causes are discussed in the following section.

2. There is an increase in the number of bacteria during the night hours, the highest numbers being attained at 3 a.m. in all except the bottom samples (Fig. 5).

Summer Series, July 23/24, 1929. From Table IIC the following observations were made :—

1. In this series, the number of surface bacteria is again relatively high and fluctuates very much between the 3-hour samplings.

2. The lowest surface numbers are at noon and the highest at 5 p.m.

3. Below the surface the numbers were fairly constant, but at 10 and at 20 fathoms there were increases after midnight (Fig. 6).

Autumn Series, October 24/25, 1929. These samples confirmed the findings of the three previous series. The following conclusions were drawn (Table IID) :—

1. The number of surface bacteria fluctuates very much, but on this occasion there were relatively few organisms in the surface water.

2. At lower levels there was in general an increase in numbers during the night, so that the bacterial content tends to be highest in the early morning hours (Fig. 7).

In summing up the results of these series of bacteriological analyses spread over a period of a year, it is seen that (i.) the number of surface organisms is usually relatively high, and is much subject to short-period variations, (ii.) in deeper water layers the bacterial content is very much lower and remains almost constant throughout the year, and (iii.) during the hours of darkness the numbers tend to increase slightly.

Results of Pollution Tests.

Conradi-Drigalski agar and McConkey agar were used as routine media for the detection of pollution. Both these media inhibit, or at least retard, the growth of all but intestinal bacteria, so that the presence of colonies on a plate inoculated from a water sample is presumptive evidence of the contamination of that water. Most of such colonies will appear red and will be the lactose-fermenting *B. coli* or its congeners. This can be confirmed by a lactose-broth culture made from the same

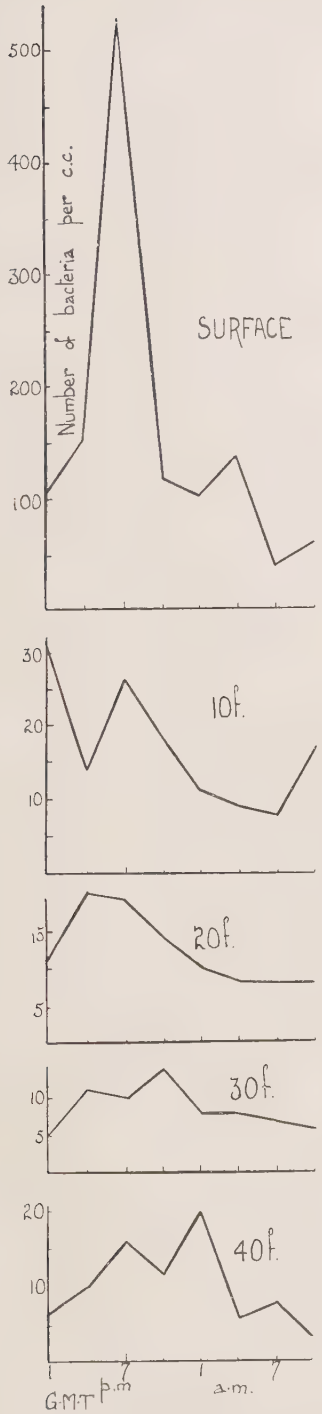

FIG. 4.—Diurnal variation in the numbers of bacteria at different depths. Samples taken 19/20.xii.29. Loch Striven.

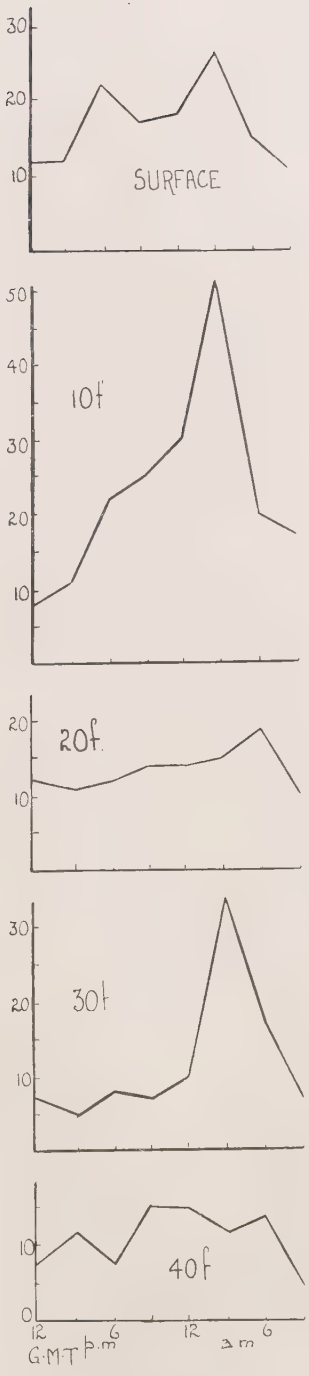

FIG. 5.—Samples taken 7/8.iii.29. Loch Striven.

water sample. The intestinal organisms, e.g. *B. typhosus*, Morgan's bacillus, which do not ferment lactose, are less common in polluted water ; on the above media they appear as blue-white colonies.

It was found that bacteriologically the Loch Striven waters were remarkably pure throughout the greater part of the year. During the winter months, however, when the herring fishing was in progress, the surface samples showed an increase in the total bacterial content, and this was due in part to an increase in the numbers of presumptive coliform organisms, when they formed about 20% of the total. When the herring season was over, however, the water became free from these organisms.

Loch Long. The results given in Table III show that at Loch Long the vertical distribution of bacteria is very similar to that of Loch Striven, though the bacterial content is in general higher. This is possibly to be connected with the greater accessibility of this loch to steamer traffic.

Here again there is little evidence of regular seasonal variation (Fig. 3). Table III shows that the bacterial content of the surface water varies widely and apparently erratically. The samples taken at other levels show a midsummer minimum, an autumn increase and a minimum in the months of January and February. Very few bacteria were present in the January samples ; at this time the temperature was so low that the waters at the head of the adjoining branch, Loch Goil, were frozen. This seems to bear out the opinion generally held that water bacteria are specially sensitive to changes in temperature.

Normally there are more bacteria at the surface than at other levels ; there is only one exception, namely, the May series of samples taken in Loch Long. Here a much higher bacterial content is found at 10 fathoms. For this there does not appear to be a suitable explanation, unless we have regard to the fact that the number of presumptive coliform organisms obtained on McConkey plates on that date was specially high and that 3 out of 4 lactose-broth cultures produced gas. This points to some special circumstances causing localised subsurface contamination of the water at the spot where the samples were taken.

Greenock. In this area the samples were taken at the deepest part of the river channel off Greenock, where the water is much polluted with sewage and with industrial effluents. The effect of such pollution will of course be more marked near the shore-line. Between the coast and mid-channel there is a certain amount of self-purification of the water ; nevertheless, the bacterial content of the open water is affected. The number of organisms per c.c. is considerably higher than in the lochs (see Table IV and Fig. 3) ; further, the number of colonies on McConkey plates is many times more than the number on gelatine and agar plates, so that it is not possible to estimate the number of coliforms without dilution of the

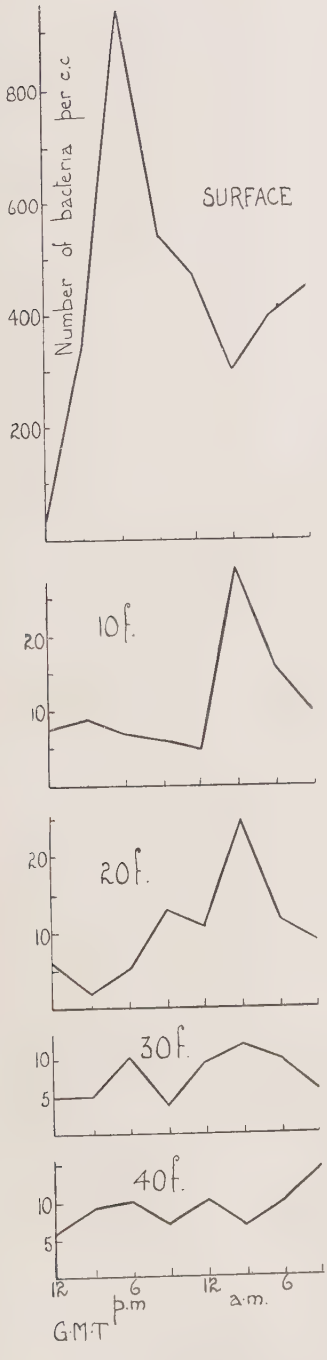

FIG. 6.—Diurnal variation in the numbers of bacteria at different depths. Samples taken 23/24.vii.29. Loch Striven.

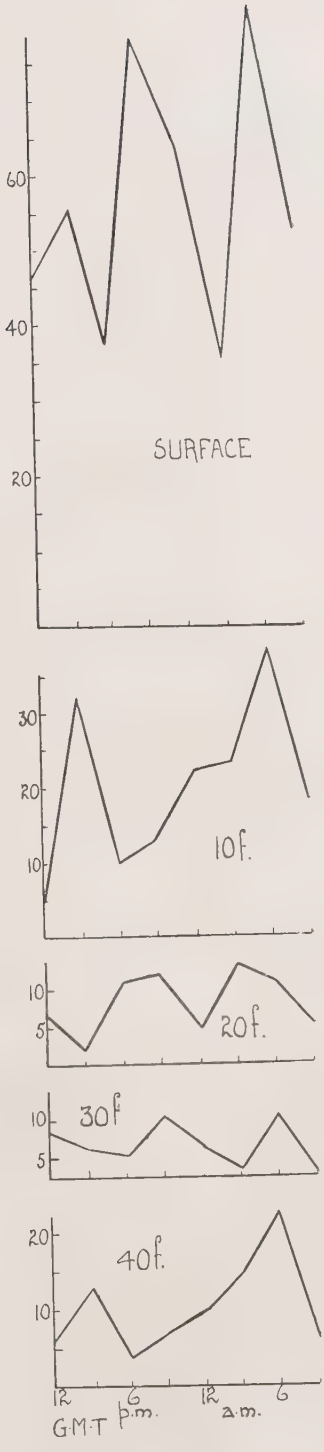

FIG. 7.—Samples taken 24/25.x.29. Loch Striven.

sample before plating. In this area then a high proportion of the constituent organisms are of the intestinal type.

The surface samples again showed by far the highest numbers; at 10 fathoms it was found always that there were fewer organisms; at the bottom, however, there was an increase. In none of these was any regular seasonal quantitative variation found.

Cumbrae Deep. At the above-mentioned stations samples could not be obtained at great depths, the deepest being 40 fathoms in Loch Striven. At Cumbrae Deep, however, there is a depth of 62 fathoms. The results from one series of samples (Table V) show that the vertical distribution is similar to those of the lochs, namely, that the surface waters have a relatively higher bacterial content, that the numbers decrease with increasing depth and that they increase again near the bottom.

It is interesting to note that the number of bacteria here is higher than it is in the lochs, but Cumbrae Deep is not typical of the Clyde Sea Area, since it is used as a dumping-ground for the Glasgow sewage treated by the activated sludge process at the Shieldhall Sewage Disposal Works. Buchanan states that such activated sludge, like crude sewage, has a bacterial flora of largely intestinal species (see **13,** p. 2); this sludge therefore appears to affect the bacterial content of the sea-water into which it is discharged.

Millport. The foregoing samples were taken in open water. For purposes of comparison, samples were taken (*a*) in the intertidal zone and (*b*) in a high-water rock pool, and the bacterial content investigated. From the results given in Tables VI and VII it is seen that the numbers of bacteria are very much higher than in the open water—a fact to be correlated with the congestion of other living organisms in the strip of water bordering the land.

Factors Affecting Distribution of Bacteria.

The foregoing work deals only with the free-living bacteria; these may be differentiated by their mode of nutrition into prototrophic and metatrophic species. It is not yet definitely established to what extent the prototrophic forms, as for example, the nitrogen-fixing bacteria, are found free-living in the sea. Ordinary marine conditions are not always favourable for their growth, so their existence is problematic. Experimental proof of their activity is available, but much of the work done on the subject is contradictory.

The majority of free-living bacteria are metatrophic, deriving their organised food-stuffs directly or indirectly from other organisms. In the sea two classes may be conveniently distinguished :—

(i.) The saprophytes living on and attached to particles of an organic nature, such as decaying seaweed, dead plankton and terrigenous detritus. This group will include the putrefactive bacteria ; they will be common where suspended matter is common and will be particularly abundant where such particles will accumulate, as for instance at the sea-bottom.

(ii.) The true planktonic bacteria, which have a simple metabolic cycle, and whose source of food is the dissolved organic material—amino-acids, proteins, and carbohydrates,—present in the sea, particularly in the surface waters near the coast-line.

(*a*) *Sunlight.* Among the physical factors affecting bacteria, sunlight is well-known to have a deleterious action on the growth of micro-organisms. This is due to the bactericidal action of ultra-violet light, and is to be distinguished from the ordinary retarding effect of light on growth. If the insolation is sufficiently intense, it would be expected that this effect would be most marked at the surface. The foregoing results for the Clyde Sea Area, however, show a greater number of bacteria at the surface, even when the samples were taken on sunny days, so that the bactericidal effect of light was apparently negligible. Schmidt-Neilsen (**23**), on the other hand, records finding at Dröbak 26 bacteria per c.c. at the surface and 420 per c.c. at a depth of 25 metres, and states that this progressive increase with depth is possibly due to the influence of sunlight. Similarly Bertel (**5**) found that off the coast of Monaco the numbers increased with depth. From two series of samples he found that the numbers increased from 1 per c.c. at the surface, (*a*) to 30 at a depth of 200 metres, (*b*) to 36 at a depth of 400 metres ; these results were obtained during the months of May and June, when insolation is intense.

In the same way, the bactericidal effect of sunlight would be expected to be more marked during the summer months, and, if it were the limiting factor, the numbers of bacteria would be lower in the summer than in the winter months. For the Clyde Sea Area, the bacterial content of the water on the whole is lower in the period from June to August, but it is not possible at this stage to correlate such seasonal variations with definite variations in the intensity of light. There do not appear to be other seasonal records with which these results may be compared.

The diurnal variation in the bacterial content may be due in part to the effect of sunlight. Tables IIA, B, C, and D show that in general there is an increase during the hours of darkness. This confirms the findings of Fischer (**10**), that more bacteria are to be found at sunrise than in the afternoon. Bertel (**5**) also states that there is a night-time bacterial increase which persists even to the early hours of the morning. He bases his conclusions, however, on the evidence of three series of samples taken

on different dates, so that it is possible that other factors came into play during the intervals. From his experimental work Bertel deduces that the night-time is more favourable for reproduction by bacteria ; but the fact that bacteria are more numerous at night does not prove that they necessarily reproduce more rapidly at night, since other factors such as the vertical mixing of water may cause movement of particles supporting bacteria from one water level to another.

(*b*) *Temperature.* An increase of temperature within certain limits favours the growth of micro-organisms in general. Sudden and marked changes in temperature may, however, have an unfavourable effect on bacteria, particularly on those species which do not form spores and which have not a highly resistant cell-membrane. Water bacteria are in general small non-sporing bacilli, notoriously sensitive to sudden changes in temperature (**2**).

Ordinarily, in the Clyde Sea Area the range of temperature variation is not sufficiently wide to show its effect on the bacterial content of sea-water. An examination of the results of the January samples taken in Loch Long shows the number to be very low ; these samples were taken during an extremely cold spell when the head waters of the adjoining loch were frozen.

(*c*) *Movements of Water.* In a still body of water it would be reasonable to expect a greater number of micro-organisms at the surface and at the bottom than in the intervening layers. However, any movements which cause vertical mixing from one layer to another may cause short-period variations in the bacterial content of the water at any depth. In view of this, it is remarkable that for the Clyde Sea Area the vertical progressive diminution in the number of bacteria is so constant.

Near land masses, especially off the steep western coast of Scotland, there is a tendency for vertical upwelling of water from the bottom and a surface flow away from the land. Foodstuffs are thus brought up to the surface, and become available for aerobic marine bacteria. At the same time, land drainage contributes its quota of detritus and soluble organic compounds, the less dense fresh water tending at first to distribute itself over the surface (**17**). Thus the surface waters appear to be best furnished with foodstuffs for the support of a more numerous bacterial population than is found at lower water levels. Almost all the samples taken illustrate this.

Tidal movements, similarly, may affect the bacterial content of the water. The results of the German Plankton Expedition (**10**) show that the number is higher during the ebb than during the flood tide. This influence is more marked when there is a slightly shelving coast-line with a comparatively broad intertidal zone which supports much plant and animal life, the number of bacteria being correspondingly high. In

the lochs investigated, however, the steeply sloping sides afforded only a narrow intertidal zone, and the tidal variations do not appear to have much effect on the bacterial content of the water. This is best shown in Tables IIA, B, C and D, where samples were taken at 3-hour intervals over periods of 24 hours at various seasons of the year.

(*d*) *Sedimentation of Organic Particles.* Attention has already been drawn to the fact that the saprophytic bacteria are not truly planktonic, but are attached to suspended organic particles of various origins. Any factor which determines the distribution of these particles will affect also the number of saprophytic bacteria. In water where there are no currents and no vertical mixing, it would be reasonable to expect at the surface an accumulation of such organic matter as has lower density than sea-water, with a corresponding accumulation of bacterial saprophytes. Similarly, the deposits at the bottom induce a high number of bacteria. In the intervening layers, however, through which suspended matter, as for example, the "plankton rain," tends to sink slowly, the number of bacteria also decreases progressively with depth.

Almost all the vertical series of samples taken in the Clyde Sea Area show this, viz., a relatively high bacterial content at the surface, with a gradual decrease till the bottom is reached, when the numbers again rise. Probably the increase at the bottom is due to the proximity of the mud which exists at all the stations. Some work now in progress has shown that the number of bacteria in the mud itself far exceeds that of the water immediately above it.

(*e*) *Biological Factors.* Since most water bacteria are heterotrophic, they will enter into competition for foodstuffs with the simpler animal forms, and will in turn be preyed upon by protozoa. It is well known that in the soil the numbers of protozoa and bacteria bear a numerical relationship to one another, namely, that when one group is abundant, the other is scarce and vice versa. It is highly probable that a similar state of affairs exists in the sea, though experimental evidence is lacking as yet.

After a period of great activity in the development of any group of organisms, there will be a glut of dead organisms and bacteria may thereafter multiply very rapidly. After the spring diatom increase in 1929, the bacterial content of the water was high, especially at the surface. There was a comparable increase during the autumn of 1928, when the herring season was in progress in Loch Striven, but not at the other stations sampled. In Loch Striven there was a great increase in the numbers of bacteria at the surface, with no corresponding increase at the other stations.

The following table shows the average number of bacteria at the surface in Loch Striven, compared with the herring catches for the season. The

latter figures are available through the courtesy of the Fishery Board for Scotland.

	1928								1929			
	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Ap.
Quantity of herrings taken monthly (crans)	0	0	49	0	0	4,644	16,841	14,075	4,727	–	–	–
No. of bacteria taken at surface in one sample per month	43	5	–	39	–	17	136	26	44	120	12	1

Thus it appears that the surface maximum in November coincides with the maximum herring catch ; this is followed by a decrease in numbers during December, and a second increase in February.

The writer wishes to make acknowledgments to the Scottish Marine Biological Association for permitting the frequent use of their boat, the *Nautilus ;* to Mr. Elmhirst, the Superintendent of their Laboratory at Millport, for readily affording facilities for work there ; to Professor D. Ellis and to Dr. J. A. Cranston of the Royal Technical College, Glasgow, for much helpful criticism and advice ; and to Mr. R. J. Nairn for frequently deputising for the writer in the collecting of samples.

SUMMARY.

1. A bacteriological survey of the Clyde Sea Area has been made over a period of a year. Water samples have been taken monthly at three stations, and also less frequently at other places. A uniform routine technique has been adopted for studying their bacterial content.

2. *Vertical Variation.* The surface waters were found to have the highest bacterial content. With increased depth until near the bottom, there was a progressive decrease in numbers. At the bottom there was usually a slight increase.

3. *Seasonal Variation.* Throughout the year the numbers were found to be remarkably constant for all layers except the surface, with only slight evidence of rhythmic seasonal variation. At the surface, the bacterial content fluctuated widely, apparently in relation to factors which are not seasonal but irregular.

4. *Diurnal Variation.* At the surface the bacterial content is irregular throughout the day ; at lower levels, there is a slight increase during the hours of darkness, the maximum occurring in the evening hours in December, and at 3–6 a.m. in March, July and October.

5. *Purity of the Water.* The waters of both Loch Striven and Loch Long were found to be remarkably free from pollution. In Cumbrae

Deep, however, and in the estuary off Greenock, the numbers of bacteria were high, and a large proportion of these were found to be presumptive coliform organisms.

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TABLE I.

Loch Striven.

No. of bacteria present, determined by colony counts of plate cultures incubated 5 days at room temperature.

Depth.	Agar Cultures.				Gelatine Cultures.				Total.	Average per c.c.
	1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.		
18/5/28										
Surface	28	34	31	36	26	–	–	–	155	43
10 fathoms	8	47	1	1	17	–	–	–	74	20
20 fathoms	4	4	0	0	3	–	–	–	11	3
30 fathoms	6	2	0	1	10	–	–	–	19	5
Bottom	1	3	1	0	2	–	–	–	7	2
15/6/28										
Surface	8	3	0	–	2	11	–	–	26	5
10 fathoms	5	3	6	–	10	13	6	–	43	8
20 fathoms	1	2	0	–	4	8	6	–	21	4
30 fathoms	0	0	0	–	6	7	5	–	18	3
Bottom	2	2	2	–	13	11	3	–	33	6
24/8/28										
Surface	43	30	28	16	36	31	7	13	204	59
10 fathoms	31	43	1	4	1	5	4	5	94	18
20 fathoms	9	9	6	1	9	11	1	5	51	10
30 fathoms	15	21	18	0	6	12	11	4	87	17
Bottom	20	16	4	4	19	22	29	7	121	23

TABLE I (*continued*).

Depth.	Agar Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Gelatine Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Total.	Average per c.c.
5/10/28										
Surface	15	24	2	0	21	17	7	1	87	17
10 fathoms	4	6	5	0	7	9	2	0	33	6
20 fathoms	9	8	–	–	3	2	–	–	22	5
30 fathoms	0	0	2	0	2	0	0	0	4	1
Bottom	0	1	0	2	2	3	1	0	9	2
2/11/28										
Surface	73	118	63	23	113	185	89	47	711	136
10 fathoms	9	18	6	1	11	5	3	1	54	10
20 fathoms	1	8	3	0	4	4	0	0	20	4
30 fathoms	6	2	1	1	3	3	0	0	16	3
Bottom	3	8	5	0	4	4	2	0	26	5
1/12/28										
Surface	27	29	5	0	33	27	12	1	134	26
10 fathoms	11	1	3	0	15	12	5	1	48	9
20 fathoms	3	8	1	0	3	1	1	1	18	3
30 fathoms	2	2	0	0	0	3	0	0	7	1
Bottom	4	7	2	0	0	1	4	0	18	3
18/1/29										
Surface	17	21	4	2	90	81	12	1	228	44
10 fathoms	2	8	4	1	10	13	7	0	45	9
20 fathoms	3	5	3	0	2	7	1	1	22	4
30 fathoms	6	6	7	0	0	7	0	0	26	5
Bottom	7	6	1	3	2	5	1	0	25	5
15/2/29										
Surface]	117	159	22	15	109	161	41	5	629	120
10 fathoms]	40	42	20	3	29	9	6	4	153	29
20 fathoms	12	15	8	2	0	15	13	11	76	15
30 fathoms	8	7	5	3	6	11	2	0	42	8
Bottom	5	9	1	1	10	3	3	0	32	6
7/3/29										
Surface	24	1	–	–	–	–	–	–	25	12
10 fathoms	10	7	–	–	–	–	–	–	17	8
20 fathoms	12	13	–	–	–	–	–	–	25	12
30 fathoms	7	7	–	–	–	–	–	–	14	7
Bottom	7	10	–	–	–	–	–	–	17	8
12/4/29										
Surface	0	1	0	0	1	1	0	0	3	1
10 fathoms	1	0	1	0	1	0	1	0	4	1
20 fathoms	3	–	2	0	1	0	2	3	11	2
30 fathoms	1	1	0	0	–	1	0	1	4	1
Bottom	4	4	2	2	1	0	0	0	13	3

Summary of Tables I and II. Loch Striven.

Depth.	Total No. of bacteria counted.	Average per c.c.
Surface	4565	80
10 fathoms	825	15
20 fathoms	433	8
30 fathoms	361	7
Bottom	417	8

TABLE IIa.

Loch Striven.

No. of bacteria present, determined by colony counts of plate cultures incubated 5 days at room temperature.

Winter Series, 19/12/28–20/12/28.

Depth.	1 p.m.	4 p.m.	7 p.m.	10 p.m.	1 a.m.	4 a.m.	7 a.m.	10 a.m.
Surface	79	131	493	123	106	97	45	53
	123	172	560	112	103	181	38	75
(Average)	101	151	526	117	104	139	41	64
10 fathoms	43	1	23	19	9	10	8	19
	18	27	29	18	13	9	9	16
(Average)	30	14	26	18	11	9	8	17
20 fathoms	13	19	17	11	12	4	9	8
	10	22	21	18	9	12	7	–
(Average)	11	20	19	14	10	8	8	8
30 fathoms	9	13	12	14	11	6	2	2
	1	10	9	14	6	11	12	10
(Average)	5	11	10	14	8	8	7	6
Bottom	9	3	15	13	–	5	8	4
	3	18	18	11	20	8	8	2
(Average)	6	10	16	12	20	6	8	3

Table IIb.

Loch Striven.

Spring Series, 7/3/29–8/3/29.

Depth.	Noon.	3 p.m.	6 p.m.	9 p.m.	Midnt.	3 a.m.	6 a.m.	9 a.m.
Surface	24	14	24	18	12	22	14	7
	1	10	21	17	26	29	17	16
(Average)	12	12	22	17	18	26	15	11
10 fathoms	10	20	11	22	29	45	22	23
	7	3	33	28	31	57	19	12
(Average)	8	11	22	25	30	51	20	17
20 fathoms	12	12	11	13	16	10	17	12
	13	11	13	15	12	20	22	9
(Average)	12	11	12	14	14	15	19	10
30 fathoms	7	3	10	4	9	33	17	6
	7	7	6	11	11	35	17	9
(Average)	7	5	8	7	10	34	17	7
Bottom	7	9	7	15	21	14	11	4
	10	15	9	15	10	9	18	6
(Average)]	8	12	8	15	15	12	14	5

TABLE IIc.

Loch Striven.

Summer Series, 23/7/29–24/7/29.

Depth.	Noon.	3 p.m.	6 p.m.	9 p.m.	Midnt.	3 a.m.	6 a.m.	9 a.m.
Surface	91	*300	*1100	*690	537	403	307	*400
	9	*400	*800	*400	409	209	494	*500
(Average)	50	350	950	545	473	306	400	450
10 fathoms	16	6	6	9	7	31	19	12
	1	13	8	3	4	27	13	8
(Average)	8	9	7	6	5	29	16	10
20 fathoms	6	1	4	18	6	11	9	11
	6	3	6	8	17	39	16	8
(Average)	6	2	5	13	11	25	12	9
30 fathoms	6	6	8	3	9	11	9	3
	4	5	12	6	6	14	11	9
(Average)	5	5	10	4	7	12	10	6
Bottom	9	2	19	2	3	9	5	20
	3	16	1	13	18	6	15	9
(Average)	6	9	10	7	10	7	10	14

* Approximate numbers only.

TABLE IId.

Loch Striven.

Autumn Series, 24/10/29–25/10/29.

Depth.	Noon.	3 p.m.	6 p.m.	9 p.m.	Midnt.	3 a.m.	6 a.m.	9 a.m.
Surface	41	59	41	66	49	32	101	61
	53	54	35	91	79	41	63	45
(Average)	47	56	38	78	64	36	82	53
10 fathoms	6	36	7	18	21	24	35	8
	4	29	13	9	23	22	42	29
(Average)	5	32	10	13	22	23	38	18
20 fathoms	6	0	14	15	6	14	7	7
	3	4	9	9	4	13	16	3
(Average)	4	2	11	12	5	13	11	5
30 fathoms	5	4	4	8	5	2	10	1
	8	5	3	8	4	0	6	1
(Average)	6	4	3	8	4	1	8	1
Bottom	7	15	4	11	8	11	12	12
	5	11	5	4	12	20	34	1
(Average)	6	13	4	7	10	15	23	6

TABLE III.

Loch Long.

No. of bacteria present, determined by colony counts of plate cultures incubated 5 days at room temperature.

Depth.	Agar Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Gelatine Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Total.	Average per c.c.
23/5/28										
Surface	39	37	8	–	40	–	18	–	142	36
10 fathoms	157	216	143	–	184	–	76	–	776	194
20 fathoms	1	0	1	–	3	–	3	–	8	2
Bottom	3	7	2	–	0	–	1	–	13	3
22/6/28										
Surface	39	10	0	–	53	48	37	–	187	37
10 fathoms	21	10	2	–	40	18	14	–	105	21
20 fathoms	5	7	0	–	9	6	4	–	31	6
Bottom	1	0	1	–	8	6	6	–	22	4
27/8/28										
Surface	35	49	0	4	10	0	1	3	102	20
10 fathoms	16	6	1	1	11	15	0	3	53	10
20 fathoms	0	1	0	0	1	4	1	0	7	1
Bottom	1	3	0	1	4	4	4	5	22	4
21/9/28										
Surface	38	70	33	8	123	89	83	5	449	86
10 fathoms	9	7	5	1	23	20	4	3	72	14
20 fathoms	9	11	3	3	1	12	6	11	56	11
Bottom	19	11	4	1	34	19	11	1	100	19
12/10/28										
Surface	39	46	33	1	41	43	3	5	211	40
10 fathoms	1	3	3	1	7	4	0	0	19	4
20 fathoms	1	5	1	0	2	3	4	0	16	3
Bottom	28	59	3	0	1	1	0	0	92	18
16/11/28										
Surface	129	107	51	5	50	43	14	12	411	79
10 fathoms	20	21	7	6	19	17	2	0	92	18
20 fathoms	3	13	4	1	0	2	5	1	29	6
Bottom	27	24	15	2	12	10	1	1	92	18
17/12/28										
Surface	90	21	8	0	29	15	7	11	181	35
10 fathoms	17	3	2	0	12	11	12	1	58	11
20 fathoms	11	13	1	2	19	18	8	1	73	14
Bottom	5	11	1	1	17	4	0	0	39	8
25/1/29										
Surface	3	3	0	0	0	4	1	1	12	2
10 fathoms	1	0	1	0	5	2	1	0	10	2
20 fathoms	3	2	0	0	8	2	2	0	17	3
Bottom	6	2	8	1	5	2	1	0	25	5
22/2/29										
Surface	81	32	41	30	33	30	3	4	254	48
10 fathoms	7	2	0	0	1	0	0	0	10	2
20 fathoms	13	12	2	6	2	9	0	0	44	8
Bottom	17	24	4	1	23	19	1	0	89	17

TABLE III (*continued*).

Depth.	Agar Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Gelatine Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Total.	Average per c.c.
1/3/29										
Surface	7	24	5	4	2	3	0	0	45	9
10 fathoms	3	1	7	1	1	0	0	0	13	2
20 fathoms	5	4	7	0	5	9	2	1	27	5
Bottom	10	9	4	2	11	5	1	1	43	8
15/4/29										
Surface	11	3	3	7	0	2	0	0	26	5
10 fathoms	9	9	9	11	3	1	1	5	48	9
20 fathoms	10	3	9	0	0	1	0	7	30	6
Bottom	8	11	1	18	1	8	1	0	48	9

Summary of Table III. Loch Long.

Depth.	Total No. of bacteria counted.	Average per c.c.
Surface	1740	39
10 fathoms	1198	27
20 fathoms	264	6
Bottom	448	10

TABLE IV.

Greenock.

No. of bacteria present, determined by colony counts of plate cultures incubated 5 days at room temperature.

Depth.	Agar Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Gelatine Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Total.	Average per c.c.
8/6/28										
Surface	103	189	–	5	409	261	–	1	968	230
10 fathoms	71	13	–	0	77	50	–	0	211	50
Bottom	12	40	–	10	56	72	–	1	191	45
28/8/28										
Surface	123	80	6	28	119	71	31	63	521	100
10 fathoms	8	17	3	6	88	93	25	34	274	52
Bottom	153	61	6	5	113	51	35	17	441	85
22/9/28										
Surface	274	502	197	112	637	531	345	149	2747	530
10 fathoms	62	33	11	2	102	73	12	2	297	57
Bottom	36	48	63	3	110	143	79	51	533	103
12/10/28										
Surface	544	476	207	90	341	191	132	103	2084	400
10 fathoms	71	112	89	13	29	41	67	20	442	85
Bottom	51	107	28	11	18	28	13	6	262	50
16/11/28										
Surface	206	217	120	49	273	233	191	53	1342	257
10 fathoms	39	20	24	13	29	35	12	3	173	33
Bottom	38	31	31	2	44	47	16	4	213	41

TABLE IV (*continued*).

Depth.	Agar Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Gelatine Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Total.	Average per c.c.
17/12/28										
Surface	121	70	51	12	326	131	49	21	781	150
10 fathoms	67	51	21	5	47	41	33	4	269	52
Bottom	113	70	51	9	71	29	12	11	367	71
25/1/29										
Surface	49	46	36	5	88	139	29	1	393	75
10 fathoms	69	119	69	19	63	130	39	13	521	100
Bottom	18	17	4	0	8	11	6	0	64	12
22/2/29										
Surface	401	317	91	35	177	210	23	7	1261	243
10 fathoms	79	91	40	9	154	115	70	0	558	130
Bottom	94	61	24	10	81	207	73	9	559	130
1/3/29										
Surface	76	201	153	71	89	331	71	41	1033	198
10 fathoms	36	119	139	25	18	17	101	24	480	92
Bottom	101	91	28	2	30	27	91	141	511	98
15/4/29										
Surface	229	89	23	8	109	6	0	0	464	90
10 fathoms	123	41	29	7	110	11	0	3	324	62
Bottom	207	22	9	17	140	2	3	0	400	77

Summary of Table IV. Greenock.

Depth.	Total No. of bacteria counted.	Average per c.c.
Surface	10,626	240
10 fathoms	3,338	71
Bottom	3,340	71

TABLE V.

Cumbrae Deep.

Depth.	Agar Cultures. 1·0 c.c.	0·5 c.c.	0·1 c.c.	Gelatine Cultures. 1·0 c.c.	0·5 c.c.	0·1 c.c.	Total.	Average per c.c.
1/9/28								
Surface	204	56	22	193	103	29	607	100
10 fathoms	11	10	1	6	0	0	28	9
20 fathoms	40	5	3	–	1	0	49	23
30 fathoms	20	5	2	2	0	1	30	9
40 fathoms	6	3	0	3	1	0	13	4
50 fathoms	11	1	0	3	0	0	15	5
62 f. (bottom)	21	13	0	–	0	0	34	16

TABLE VI.

QUANTITATIVE BACTERIAL ANALYSES OF LITTORAL SURFACE SAMPLES TAKEN IN THE FUCUS ZONE, CRAN BIGHT, OUTSIDE THE MILLPORT MARINE BIOLOGICAL STATION.

Date of Sample.	Agar Cultures. 1·0 c.c.	1·0 c.c.	0·1 c.c.	0·01 c.c.	Total.	Average per c.c.
31/3/28	442	457	91	0	990	470
2/4/28	∞	227	181	227	408	> 500
3/4/28	238	104	101	8	451	210
4/4/28	201	–	15	5	221	220
5/4/28	130	–	44	0	174	170
6/4/28	521	479	71	1	1072	550
7/4/28	89	198	21	0	308	150
8/4/28	514	347	66	–	927	440
9/4/28	193	85	10	10	298	140
10/4/28	503	200	–	–	703	350
11/4/28	371	366	–	–	737	370

Approximate mean average number of bacteria per c.c. = 500.

TABLE VII

QUANTITATIVE BACTERIAL ANALYSES OF SURFACE SAMPLES TAKEN FROM AN ENTEROMORPHA POOL OUTSIDE THE MILLPORT MARINE BIOLOGICAL STATION.

Date of Sample.	Agar Cultures. 0·1 c.c.	0·1 c.c.	0·01 c.c.	0·01 c.c.	Total.	Average per c.c.
31/3/28	494	593	61	27	1175	5300
2/4/28	731	448	59	73	1311	6000
3/4/28	728	568	81	35	1412	6400
4/4/28	381	473	51	92	997	4600
5/4/28	640	341	49	50	1080	4900
6/4/28	760	451	60	81	1352	6100
7/4/28	331	307	52	70	760	3500
8/4/28	800	488	60	23	1371	6200
9/4/28	411	571	21	82	1085	4900
10/4/28	566	498	20	27	1111	5000
11/4/28	470	403	21	72	966	4400

Approximate mean average number of bacteria per c.c. = 5200.

Note on the Distribution of *Lichina confinis* and *L. pygmæa* in the Plymouth District.

By

Gladys L. Naylor, B.Sc.

With one Chart.

Introduction.

Very little work has as yet been done on the occurrence and distribution of marine lichens in the Plymouth district. The present investigation of the genus Lichina was undertaken at the suggestion of Dr. J. H. Orton, who, having noticed the two Lichina species at New Train Bay near Padstow, North Cornwall, thought it might be of interest to determine their distribution in the Plymouth area.

The characteristic appearance of the Lichina vegetation is too well known to require more than a brief mention (**10**). Both are small fruticose lichens with densely branched, dark-coloured thallus. *L. confinis*, the smaller of the two, has rounded branchlets barely 3 mm. long, and forms small patches 2–4 cm. across, while *L. pygmæa* has slightly longer branches, up to 10 mm. in length, with flattened lobes, and may form circular patches varying from a few inches to a foot or more in diameter. In colour *L. confinis* is black or very dark brown, but *L. pygmæa*, though usually very dark, may occasionally be light brown or greenish in colour.

The definite zones occupied by these two lichens on the shore are also well known, and have been recorded by Nylander (**7**), Joubin (**4**, p. 13), Cotton (**2**, p. 26), and Knowles (**6**, p. 105). On most rocky coasts the zone immediately above mean high water is colonised by the black crustaceous lichen *Verrucaria maura*, the lower limit of which is bounded by the brown alga *Pelvetia canaliculata*. *L. confinis* occurs at the upper limit of the *V. maura* zone where this overlaps the belt of orange lichens (for detailed account see Knowles [**6**, p. 101]), and is not strictly marine, though exposed to spray and probably to occasional immersion by very high tides. The vertical width of the *L. confinis* zone varies with the exposure, being greatest where there is a wide spray zone. *L. pygmæa*, on the other hand, never occurs above the Pelvetia zone, but is usually most abundant a little below it, though it may be present down to low neap-tide level (**2**), (**6**). This lichen is truly marine, and is incapable of surviving the desiccation to which *L. confinis* is often exposed.

The rocks round Plymouth Sound are chiefly Devonian (13), consisting for the most part of slates, grits and shales, the strata running at various angles but often nearly vertical; volcanic rocks occur at Rum Bay and Drake's Island, felsite at Kingsand; the shore below the Hoe, Tinside to Devil's Point, is limestone, this rock also occurring at Mount Batten and the north-west end of Drake's Island, while there are two further exposures, one at Cremyll and a small one below Mount Edgcumbe.

Localities Investigated.

The localities investigated include all the shores skirting the Sound itself, from Reny Rocks to Batten Breakwater, Tinside to Devil's Point, Cremyll to Penlee Point, as well as Drake's Island and the Breakwater, and outside the Sound as far as the mouth of the River Yealm to the east and from Penlee Point to Rame Head and Whitsand Bay (Polhawn Cove) to the west (see Chart). These localities will be considered briefly below, working from east to west, with the exception of the calcareous rocks which will be taken together at the end.

River Yealm to Ram's Cliff. Both species of Lichina occur all along this part of the coast, the width of the zones varying chiefly with the slope of the foreshore. Where the rocks are steep, as to the east of Wembury Church, and at Staddon Point, the lichen zones are well developed, but where the foreshore is flatter the zoning is not so marked, and with the restriction of the spray zone *L. confinis* is less abundant, as for example between Wembury Church and Reny Rocks. Both species are necessarily absent from the sandy bays at Wembury and Bovisand, and *L. pygmæa* is also absent from the protected part of the south bank of the River Yealm. Throughout the area both species are usually found on the south and west faces of the rocks, these being the sides exposed to greatest wave action and insolation.

Ram's Cliff to Mount Batten (Jennycliff Bay). This area is interesting because of the entire absence of *L. pygmæa* between Ram's Cliff and a point just south of Batten Breakwater. The disappearance of *L. confinis* is not complete, but this species becomes steadily less common to the north of the Bay. The coast here is much less exposed than the part previously considered, lying as it does well within the Breakwater and facing west. The central part of the Bay is rather flat, with some sandy beaches, but numerous steep rocks also occur, especially towards Ram's Cliff. Owing to the decreased exposure and more level foreshore, the less steeply inclined rocks are covered with a dense growth of seaweeds, the different zones of which overlap; this would effectually prevent the establishment of *L. pygmæa* which seems to require a good supply of light and air.

Chart of the Plymouth District showing the distribution of *Lichina confinis* and *L. pygmæa*.

Continuous line —— *L. pygmæa*
Dots . . . *L. confinis*.

There are many rocks, however, especially towards Ram's Cliff, which appear to be eminently suitable for the growth of this lichen, having steep faces, barnacle-covered, but bare of fucoids, the competition factor being thus removed. The small red seaweed, *Catenella opuntia*, which normally occupies the same zone as *L. pygmæa* but on the shady sides of the rocks, is abundant here even on the less shady surfaces, and this would indicate, however, that the insolation of this part of the shore is less intense than might be supposed, and possibly this, combined with decreased exposure to wave action, is enough to account for the absence of the lichen.

The Cattewater and the Hamoaze. Neither of these areas was investigated in detail, but *L. pygmæa* is certainly absent from the Cattewater; both this area and the Hamoaze are sheltered from direct wave action, and as the latter also offers few if any rocky situations such as are necessary for the growth of *L. pygmæa*, it is probable that this lichen is absent from here also.

Cremyll to Redding Pt. (Mt. Edgcumbe). Both species of Lichina are rare along this part of the shore, which, like Jennycliff Bay opposite, is very sheltered. From Cremyll to Raveness Point the foreshore consists chiefly of pebble beaches, but at Raveness Point the cliffs jut out into the water, and at this point only does *L. pygmæa* occur as two or three small patches on a limestone rock. Between Raveness and Redding Points the Staddon grits which form the bulk of Mount Edgcumbe, and which reappear at Picklecombe Point, give place to river gravel, which forms a boulder beach from which *L. pygmæa* is entirely absent, though *L. confinis* appears occasionally.

Redding Point to Cawsand. From Redding Point the coast bears away west and is exposed to much more direct wave action. About halfway between Picklecombe Point and Kingsand the grits give place to felsite which forms a much flatter, less dissected foreshore. *L. confinis*, though locally very abundant on the grits, hardly occurs along the felsite, the rocks being too low to form a suitable spray zone, and the lichen does not, in this district, make use of occasional immersion by spring tides by growing at a lower level than usual (**2**, p. 28). *L. pygmæa* is abundant all the way along and shows a decided preference for the sunny side of the rocks.

Cawsand to Penlee Point. This stretch is again marked by the absence of *L. pygmæa* although *L. confinis* occurs quite abundantly. The coast faces north-east, and the wooded cliffs dip very steeply to the water. Exposure both to wave action and insolation is therefore low, and this is emphasized by the abundance of *Catenella opuntia* even on the exposed surfaces of the rocks.

Penlee Point to Whitsand Bay. All along this part of the coast the Lichina vegetation is very well developed. The rocks, which consist of Dartmouth slates, form steeply inclined surfaces, barnacle-covered, and the exposure is too great to allow the growth of seaweed to any great extent. *L. pygmæa* forms a well-marked zone, 4–5 ft. wide vertically, the individual patches sometimes occupying an area of two or three square feet — as at Polhawn Cove, Whitsand Bay. *L. confinis* shows a vertical range of 2–3 ft. between Penlee and Rame Head, but is less abundant in Whitsand Bay. Although the exposure of this part of the coast is great, the actual cliff face is low, and therefore the spray zone is comparatively narrow, and this possibly accounts for the restricted vertical range of *L. confinis* in this district as compared with its range at Clare Island (**2**) and Howth (**6**).

Drake's Island. The rock here is mostly volcanic, but at the north-west end is a small mass of limestone. On the sheltered north shore there are two or three small sand and pebble beaches, but with these exceptions the foreshore is short and the rocks rugged. *L. pygmæa* is entirely absent from the north and north-east sides, but appears on the east and is abundant all along the southern shore. On the limestone mass, the more or less level top of which about corresponds to the Pelvetia zone, *L. pygmæa* occurs occasionally on the edges of small sunny pools. *L. confinis* is comparatively rare on the island, though it appears at intervals along the southern side. It seldom grows on flat surfaces, but prefers cracks and hollows on the seaward side of the rocks.

The Breakwater. The upper level of the Breakwater is below the *L. confinis* zone, and this lichen is therefore absent, but *L. pygmæa* is well represented on the sloping seaward face, the exposure of which is too great to permit a dense growth of seaweed. *L. pygmæa* shows a vertical range of about 4–5 ft., the region of greatest abundance being in the upper middle part of the zone : it is especially frequent along the upper and lower edges of the limestone blocks of which the Breakwater is built, but where the surface of these is very rough it may cover them more or less entirely. It is usually associated with a good deal of Enteromorpha and Porphyra. It is entirely absent from the two ends of the Breakwater which are built up with a horizontal surface in the *Fucus platycarpus* zone — that is, just below the Pelvetia level ; neither does it occur at all along the inner north-facing side of the Breakwater, which, though more steeply inclined than the outer face, is protected, and along which the brown seaweeds form a more or less continuous covering.

Calcareous rocks. The calcareous rock of the district takes the form

of hard limestone, on which the lichen flora is thin and poorly developed in most places, with fewer orange forms, while the *Verrucaria maura* belt is ill-defined or lacking (**6**, p. 116). The calcareous areas investigated include Mount Batten, Tinside, Firestone Bay, and Devil's Point.

Mount Batten. Neither species of Lichina occurs on Batten Breakwater itself, and indeed they are but poorly represented in this locality. *L. confinis* grows thinly in the crevices of rocks exposed to spray, but is never common; *L. pygmæa* is present for a few yards on the south-west face at the limit of the main limestone mass, and a few patches of this species also occur among the Pelvetia plants on the seaward side of some high rocks further down the beach. *V. maura* is similarly scanty, and favours shady places, also growing rather lower on the rocks than usual.

Tinside. The lichen vegetation of this area is very scarce altogether: *L. confinis* does not occur at all, *V. maura* is scanty, being present in the more shady and sheltered places only, and *L. pygmæa* is only found here and there. The limestone of this part is worn into innumerable small pockets, and it is chiefly in these, at a level corresponding to the upper Pelvetia zone, that *L. pygmæa* occurs. The pockets probably remain moist for a considerable time, but it is noticeable that the situations are usually exposed to the sun.

Firestone Bay and Devil's Point. *L. confinis* is comparatively rare throughout this area, only appearing on the rocks most exposed to spray, and even on these it is confined to a very narrow zone. *L. pygmæa*, however, is quite common, its zone of occurrence ranging from the upper Pelvetia to the upper *Ascophyllum nodosum* zones, i.e. about 3 ft. vertically. It is most abundant where the algal vegetation is not well developed, that is, on the more exposed rocks, but it may also be present in rather more shady situations, as around the bases of the Pelvetia or *Fucus platycarpus* plants. The centre of Firestone Bay consists of an artificial frontage of large limestone blocks, from which both species of Lichina are absent, although *V. maura*, and the brown seaweeds grow well on the sides of the stones.

Discussion.

Both species of Lichina are to be found abundantly in many parts of the Plymouth district, and their absence from others can probably be accounted for by a consideration of environmental conditions more especially with regard to exposure both to wave action and insolation.

Lichina confinis is the more generally distributed of the two species, occurring more or less all round the shore wherever there are rocks exposed

to spray. An exception might be noted in the limestone area of Tinside where *L. confinis* does not appear to be present. No part of the area investigated, with the possible exception of Rame Head, is subjected to very great exposure, and in all parts the actual cliff face is low, the spray zone being therefore restricted. It is probably due to this that, though so widely distributed through the whole locality, the vertical range of this lichen here is so narrow, rarely exceeding 2–3 ft., and often less than this, as compared with 12–15 ft. at Clare Island (**2**), and 50 ft. or more at Howth (**6**). Another point which might be noted is that as Plymouth is further south than these Irish localities, the desiccation to which the lichen is subjected during the summer months is probably greater in the former district. The absence of the species from the limestone of Tinside, which receives little spray in the summer, and its but scanty growth in the other limestone areas, also its comparative abundance along the tree-shaded rocks between Cawsand and Penlee, seem to emphasize that moisture is a limiting factor in the distribution of this lichen in the Plymouth district.

Lichina pygmæa. The occurrence and distribution of this lichen at Plymouth are similar in many particulars to those at Clare Island and Howth, but differ slightly in detail, more especially with regard to extent of vertical range. The chief points which correspond in all three areas are summarised below :—

1. *L. pygmæa* is most abundant on rocks which have steeply inclined faces, though it may occur on horizontal surfaces in certain situations.

2. It prefers rough surfaces and is abundant on barnacles.

3. It grows best in exposed and semi-exposed positions, the action of breaking waves seeming to be of special importance since the lichen is absent from protected situations.

The vertical range of *L. pygmæa* as seen on the Plymouth shores would appear to be more restricted than in the Irish localities, although there is no great difference in the vertical range of the tides at the three places, the smallest being at Howth with a 12 ft. spring-tide range as compared with 16 ft. at Plymouth and Clare Island. *L. pygmæa*, in the Plymouth district, extends from the upper Pelvetia zone to half-tide level only, but never as low as low neap tide, with its area of greatest abundance corresponding approximately to Mean High Water Neaps—that is, just below the *Fucus platycarpus* zone. It never occurs as undergrowth to *F. vesiculosus* or *A. nodosum*, though in some parts, as at Devil's Point, it grows around the base of *P. canaliculata* and *F. platycarpus* where these do not form a dense covering. In the places where *L. pygmæa* is most abundant there is little or no growth of the larger seaweeds, the steep rock surfaces being presumably too exposed for these plants to survive the action of the waves. Even Pelvetia and *F. platycarpus*, the least affected by exposure (**2**, p. 24), are sometimes absent, *L. pygmæa* forming the only macroscopic

vegetation, as at certain parts of Drake's Island and between Penlee and Rame Head.

Of the factors affecting the growth and distribution of the lichen considered, exposure to wave action is probably of greatest importance, though insolation, foulness of water, and salinity may also play a part. It is not easy in this district to get any clear idea of the effect of insolation, since it is only the southern shores which are directly exposed to breaking waves, and hence the absence of *L. pygmæa* from less highly insolated parts facing northwards may be due rather to the protection from wind and wave action than to decreased light intensity. This is supported by the observations of Joubin (**4**, p. 13) at the Ile de Bas, off the north coast of Finistère, where *L. pygmæa* grows freely on the exposed north and west shores, but is absent from the sheltered south side. He does not, however, give any details as to the aspect favoured by the lichen in the more exposed situations. On the west coast of Inverness-shire *L. pygmæa* is absent from the shores of sheltered sea lochs, but occurs abundantly along the coast outside, and in these exposed situations it is certainly not confined to the most highly insolated aspects so long as the surface is exposed to breaking water. Whether it is the actual mechanical stimulus of the moving water, or the high aeration—the water being not only fully saturated with dissolved oxygen as are all the surface waters of the sea, but having also a high content of air bubbles—it is certain that exposure to wave action plays a very important part in the distribution of *L. pygmæa*. The significance of light in the economy of the lichen, apart from its direct effect in photosynthesis, may lie rather in the need for a certain degree of drying-out of the thallus between tides, which could only be obtained on the better-lighted, bare rock surfaces. Such periodic drying-out is certainly essential in the case of many of the seaweeds of the foreshore. The effects of foulness of water, and salinity, have not been investigated ; the degree of exposure demanded by this lichen makes its absence from such sheltered areas as the Cattewater and the Hamoaze easily accountable without supposing any inhibition due to foulness of water or low salinity, although these may have some secondary effects.

Fruiting of *L. pygmæa* occurs freely throughout most of the district, but is less common among the Tinside and Mount Batten specimens.

SUMMARY.

The occurrence and distribution of the lichens *Lichina confinis* and *L. pygmæa* have been investigated for the Plymouth district. Both species occur frequently throughout the area. *L. confinis* is the more generally distributed, being present, though sometimes scantily, on most of the coast with the exception of Tinside ; on the exposed shores

outside the Sound itself it forms a zone 2–3 ft. wide, being especially common between Penlee Point and Rame Head. *L. pygmæa*, though very abundant on the open coast, is scanty or entirely absent along the sheltered parts of the Sound, as from Cawsand to Penlee, Cremyll to Redding Point, Jennycliff Bay, etc.

The distribution of the two species of Lichina in this district emphasizes the importance to both of the degree of exposure to wave action to which the situation is subjected. The importance to *L. confinis* lies in the height to which the spray is flung up the rocks, since occasional wetting by salt water is essential to this species. In the case of *L. pygmæa*, mechanical stimulus, aeration of water, and probably the removal of the competition factor—the larger fucoids being unable to maintain a footing on steep exposed rock surfaces—all play a part. The effect of light would appear to be secondary, and is probably of importance as connected with the desiccation of the lichen thallus between periods of immersion.

I should like to take this opportunity of expressing my gratitude to the Council of the Marine Biological Association for allowing me to work at the Plymouth Laboratory, and also to thank Dr. E. J. Allen and the members of the Staff for their kindness. I am especially indebted to Dr. J. H. Orton and Dr. W. R. G. Atkins for advice and criticism.

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On Abnormal Conditions of the Gills in *Mytilus edulis*. Part I. On Permanent Natural Reversal of the Frontal Cilia on the Gill Filaments of *Mytilus edulis*.

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With 35 Figures in the Text.

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Introduction.

A heavy percentage of the mussels obtained from various parts of the Fal Estuary, during October and November, 1927, had the gills in an exceedingly abnormal condition (31·8% among 1488 recorded). Occasional mussels from other localities (Padstow, Teignmouth, Yealm, Saltash) have been observed to have slightly abnormal gills, though perhaps in the majority of these the condition was due to the presence of a large female pea-crab, *Pinnotheres pisum*. In the Fal Estuary mussels the abnormal conditions were doubtless correlated with some factor in the environment, the percentage of pea-crabs in these being so low (4·8%) that their presence could have no relation to the abnormal condition of the gills.

These abnormal conditions will be described in some detail as they are thought to be of considerable general interest for experimental work.

The present paper will be restricted to a description of the permanent reversal of the frontal cilia on the gill filaments. In a further paper it is hoped to deal with: (1) folding over of the free edge of the gill with concrescence, (2) fusion of filaments side by side, and (3) enlargement of filaments.

The Permanent Natural Reversal of the Frontal Cilia on the Gill Filaments of *Mytilus edulis*.

Perhaps the most interesting of the abnormal conditions for experimental work is the occurrence of supernumerary food grooves on the surface of the gill (see Fig. 2, p. 921), accompanied in most cases by a permanent reversal of the frontal cilia, generally on that part of the lamella between the main and secondary grooves. The supernumerary

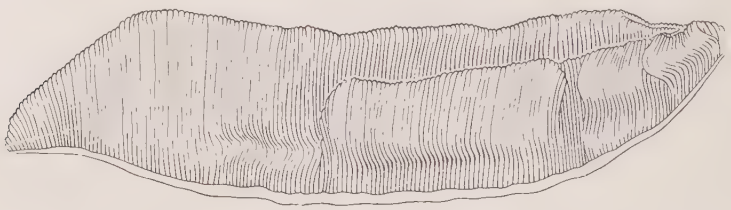

Fig. 1.—Sketch of the right inner gill of an uninfected* *Mytilus edulis* from Trelissick Reach, Fal River, showing a large fold—composed of three folds in series—on the ascending lamella. From preserved material. ×3.

groove may be set directly on the frontal surface of the lamella, as in Fig. 7, III, p. 930, or may be raised on a slight projection (Fig. 23, p. 948), or the lamella may be produced into a tiny fold (Fig. 35, II, p. 963), passing in some cases into a pocket (Fig. 30, II, p. 954). Food collected in any of these secondary grooves is passed eventually into the main grooves without interfering with the normal functioning of the gill.

These conditions were of rather rare occurrence among the Falmouth mussels, and—when found in mussels from other localities—are undoubtedly in most cases, as will be shown later, due to injury caused by the presence of a large female *Pinnotheres pisum*.

There is considerable range of variation in the size of the folds or pockets. The greatest development of pockets—indeed they are so large as almost to merit the term secondary gills—occurred on the gills of a small uninfected* mussel, 5·1 cm. long, from Trelissick Reach, Fal River. The gills were roughly 33 mm. long and 8 mm. deep; the secondary gills occurred on the ascending or reflected lamellæ of the inner

* "Infected" and "uninfected" means infected and uninfected with *P. pisum*.

gills,* that on the left gill was about 24 mm. long and 4 mm. deep ; that on the right about 18 mm. long and 4 mm. deep was composed of three pockets in series (Fig. 1). The descending or direct lamellæ of these gills were nearly normal, only a very little fusion of filaments side by side occurring. (The nomenclature employed for the gill filaments is that figured on p. 226, *Treatise of Zoology*, Vol. V, Mollusca, edited by E. Ray Lankester.) The ascending lamella of the left outer gill had a pocket about 7 mm. long and 3 mm. deep near the posterior end, and near the anterior end a simple secondary groove about 9 mm. long running into the main groove very near the mouth. A pocket about 10 mm. long and

Fig. 2.—Sketch of part of a gill of an uninfected Mytilus from Trelissick Reach, Fal River, showing a series of small folds or pockets on the ascending lamella. From preserved material. ×4.

5 mm. deep, and a simple secondary groove about 13 mm. long occurred on the right outer gill in similar positions to those on the left. The descending lamellæ of both gills were nearly normal, a very little fusion only occurring. The supernumerary pockets and grooves were arranged in such a symmetrical manner as to make it appear doubtful whether they were due to abnormal conditions in the environment.

Figure 2 is a sketch of a series of small pockets on the gill of another mussel from Trelissick Reach, Fal River, which again did not contain a pea-crab.

The gills of a Padstow mussel harbouring a female *P. pisum* (12 mm. carapace width), had numerous secondary grooves, which were almost entirely restricted, in an unusual manner, to the descending lamellæ of all four gills, as though the crab had been scrambling between the two gills of each side (Fig. 3).

* For convenience in description the two demibranchs on each side of the body are considered as two gills.

Possible Cause of Formation of Secondary Grooves and Folds.

Owing to pressure of other work at the time the Falmouth mussels were received they were preserved after no more than a cursory examination. The following observations on the structure of secondary grooves and folds and their ciliation have been made on those which may occur exceedingly rarely on gills of normal, healthy, uninfected mussels, but

Fig. 3.—Photograph of a mussel (10·0 cm. long) from Padstow, showing numerous secondary food grooves on the descending lamellæ of the gills. In some places the free edge of the two right gills is permanently folded over. From preserved material.

more frequently on the gills of mussels which harbour a large female *P. pisum*.

In working on Pinnotheres since October, 1927, a look out had been kept for any possible direct harmful effect of the crab on its host, and it had been noticed that the gills of mussels containing large specimens were sometimes injured, though it has not been found so far that the pea-crab injures the mantle causing the nacreous layer to be dissolved away, as described by Wright (**43**, p. 145). Mussels with injured gills and containing crabs, have been obtained from the River Yealm, the estuaries of the Hamoaze (Saltash), Padstow, and Teignmouth ;

those from the Fal were so commonly abnormal that it was impossible to distinguish abnormality possibly due to the presence of a pea-crab. No careful record of the frequency of injury, however, had been kept until the last two batches of mussels from Padstow were examined. These gave the following results :—

Date. 1929	Total number of mussels.	(a) No. of mussels with large pea-crabs.	No. of gills of (a) affected.	(b) No. of mussels with small pea-crabs.	No. of gills of (b) affected.	Gills abnormal, no crabs present.
June 6	944	88 (crabs with carapace width 9·0–14·0 mm.; eight were accompanied by males)	65 (73·86 %)	85 (crabs with carapace width 1·45–7·25 mm.)	0 (0·0 %)	12 (1·56 %)
Aug. 9	508	34 (crabs with carapace width 8·0–13·0 mm.; three were accompanied by males)	29 (85·29 %)	86 (crabs with carapace width 2·0–7·0 mm.	4 (4·65 %)	3 (·77 %)

Included under gills affected are mussels with (1) gills simply short, (2) gills folded over slightly at the free edge, (3) fusion of filaments, and (4) secondary grooves and folds. It may be pointed out that where gills are abnormal in mussels containing only a small pea-crab or none, there is the possibility that the injury may be due to a previous infection.

A large *Modiolus modiolus* from the Salstone, Salcombe, containing a female *P. pisum*, about 13 mm. carapace width, had not only the gills of both sides injured but also the mantle of one side. In Modiolus, however, the mantle is much thinner than is usual in healthy *Mytilus edulis*, for it appears that in the former the gonad does not encroach on the mantle.

Judging by the usually restricted area of injury—it is extremely rare for the gills of both sides to be damaged—it would seem that large pea-crabs move about very little in a mussel. On opening a mussel they are generally found on one of the inner gills mostly near the base of the foot, but just beyond the reach of the outstretched palps, and backing on the visceral mass. Beneath the crab the inner gill of the infected mussel is often considerably narrower than normal; sometimes the outer one may also be slightly narrow in this region. The shortness may be restricted to a small semicircular area (Figs. 13, I, p. 937, and 17, I, p. 943), or may extend for almost the entire length of the inner gill (Figs. 7, I, p. 930; 20, I, p. 946; 22, I, p. 947). In some cases, except for the shortness, the gill appears normal, in others the food groove is very irregular, and a slight folding over of the edge may occur with some fusion to the lamella (Fig. 4); in some places a food groove may be entirely absent for a short distance so that food collected posterior

to the break will not reach the oral end of that gill, possibly however at the break food strings will be carried on to the deeper outer gill and reach the palps that way.

In connection with the shortening of the gill there are, in perhaps the majority of cases, to be found small secondary grooves and folds or pockets. They may occur on the inner much shortened gill and on the inner face (descending lamella) of the outer gill, where it is exposed to possible injury by the pea-crab, owing to the shortness of the inner gill (Figs. 12, I, p. 936 ; 17, I, p. 943), but are not always restricted to these areas and may occur on gills of normal depth (Fig. 14, I, p. 938). The secondary grooves vary much in length, a tiny one involving only one grooved filament is shown in Figure 13, II (p. 937), while one 16 mm. long has been seen.

It is thought that these secondary grooves arise in some way as the

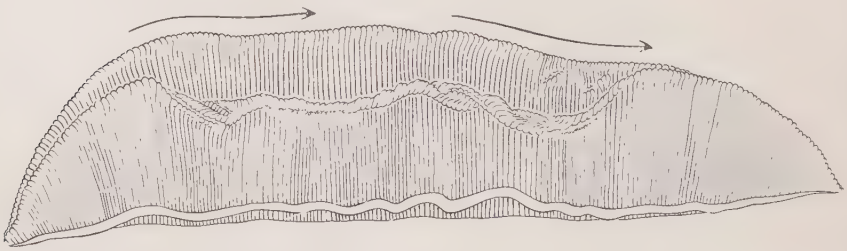

Fig. 4.—View of gills of the right side of a Padstow mussel, which harboured a large ♀ *Pinnotheres pisum*. The inner gill is short for most of its length, the free edge is in part folded over : in one place a food groove is wanting and considerable fusion of the filaments has occurred, while elsewhere secondary food grooves are present. Three short secondary grooves are present on the descending lamella of the outer gill. The arrows indicate the direction of the current in the main food grooves at the free edges of the gills. Drawn from life. ×2.

result of injury caused by the presence of the pea-crab. A pea-crab is often very difficult to remove from a gill without injury to itself or the gill, as when disturbed it hooks the pointed claw-like tips of its legs well into the gill. Whether the pockets are caused by the pea-crab hooking its claws into the gill and drawing it up into folds, which become permanent, or whether the folds grow as the result of wound stimulus, following a simple tear, can only be determined by experiment. The pockets or folds, however, are permanent. In all those examined it has been found that only the lamella on which the groove occurs is involved in the groove or fold : in some of the folds there is a bend in the non-groove-bearing filament (Figs. 23, p. 948 ; 35, II, p. 963) which seems to point to the possibility that the filaments on which the pocket occurs have been mechanically pulled into a fold, or that growth of the filament in its normal

direction has been restricted or has ceased, while that of the uninjured filament has proceeded normally. In connection with pockets and secondary grooves there is often considerable growth of inter-filamentar junctions, which of course does not occur normally in *Mytilus edulis*. (Cf. *Margaritifera vulgaris* **20**, p. 227, and *Avicula argentea* **38**, p. 155, with ciliated discs and inter-filamentar junctions.) This makes the stripping of such pockets, filament by filament, impossible without careful micro-dissection, which was not attempted, only those with little inter-filamentar growth being examined thoroughly. The two filaments of a fold are not only often strongly connected with each other, but a filament may be connected with one in the opposite lamella other than its pair; also there may be fusion of filaments side by side. In fact, wherever there is a fold or secondary groove on a gill there is a strong tendency for fusion and inter-filamentar, as well as inter-lamellar, growth to occur, especially in pockets the filaments of which are somewhat askew.

In some instances it would seem that originally deep pockets have become fused with the main lamella, little more than the secondary groove remaining, along with a greater width of the filaments and a greater number of ciliated discs for a certain distance dorsal to the secondary groove, to indicate what has occurred. Stages in this possible process are shown in Figures 5, I–II; 26 (p. 950); and 5, III. In Figure 5, I, the pocket is distinct, in Figure 5, II, the two contiguous filaments, one belonging to the main lamella and the inner one of the secondary pocket, have fused for a certain distance so that it appears that there are three filaments. In Figure 26 (p. 950) the fusion has gone a step further, and in Figure 5, III, there are only two filaments, except for a short distance, but by the structure it may be seen that the part of the filament which is dorsal to the secondary groove is formed by the fusion of filaments. This type of pocket will be referred to again in connection with its ciliation.

The cavity of pockets has always been found to face toward the free edge of the gill, but when the secondary groove is carried on only a slight elevation of the lamella it has been noticed, once or twice, that there may be a slight tendency for the process to slope dorsally (Figs. 3, p. 922); 22, II, p. 947).

When a secondary groove occurs very near the main groove it is often found joining the latter at one end, and that most usually the anterior end. In Figure 35, I (p. 963), however, a secondary groove is shown which joined the main groove and then diverged. Secondary grooves near the main groove may very occasionally join the latter at both ends.

In secondary grooves on the surface of the gill one or two filaments at either end of the groove are usually raised into a projection in continuation of the groove (Fig. 10, II, p. 934), though rarely the secondary groove

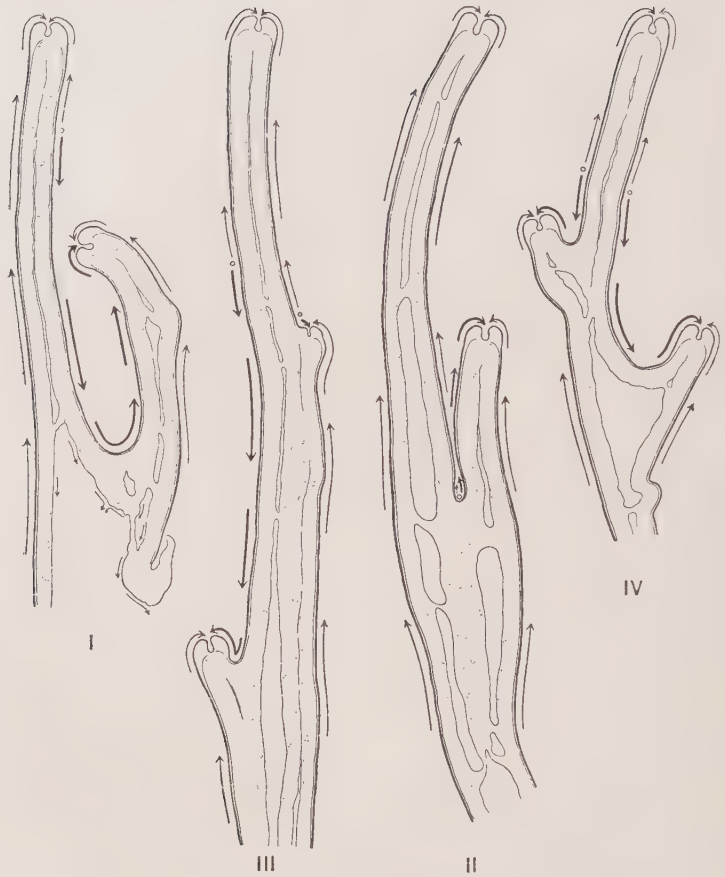

Fig. 5.—Lateral views of living filaments, bearing secondary grooves and folds, from four specimens of Mytilus from Padstow. The direction of beat of the frontal cilia is shown by arrows; heavier arrows are used when the direction is the reverse of normal. × ca. 9.

I. Filament from a deep fold or pocket on the ascending lamella of a left inner gill. The fold was near the posterior end of the gill, near the posterior adductor muscle.

II. Filament from a fold on the ascending lamella, inner gill of a Mytilus, which did not harbour a pea-crab. The fusion of adjacent parts of the filament has caused partial obliteration of the fold.

III. Filament from an outer left gill with secondary food grooves on the descending and ascending portions of the filament. That on the ascending filament (to the right) was apparently originally at the edge of a deep fold, but almost complete fusion of the filaments forming the fold has taken place.

IV. Filament from a left inner gill with secondary folds on the descending and ascending parts of the filament.

begins and ends abruptly, the preceding and following filaments being perfectly normal.

Gills have very occasionally been found with secondary grooves on the descending and ascending lamellæ of the same gill, a certain number of filaments being common to both (Fig. 5, III–IV, p. 926). Two secondary grooves one above the other on the same lamella are shown in Figures 20 (p. 946) and 22 (p. 947), while in Figure 3 (p. 922) several occur in series across the depth of the gill.

General Ciliation of Filaments Bearing Secondary Grooves.

Gills bearing a secondary groove show, over a certain area of the lamella between the main and the secondary groove, in the majority of cases, a reversal in the direction of food transportation caused by a reversal of the frontal cilia. Food particles drawn on to the gill surface instead of passing in the normal direction towards the main groove at the ventral edge of the gill, for a certain distance ventral to the secondary groove pass in a reversed direction into the secondary groove (see Fig. 9, I, p. 932). (For the ciliation and currents on the gill of *Mytilus edulis* see Orton, **29**.)

In the secondary groove the food current is always in the same direction as that of the main groove, that is towards the oral end of the gill. In secondary grooves, which do not join the main groove at their anterior end, particles debouching on the first filament with normal ciliation are carried along it into the main groove. Secondary food grooves on a gill therefore interfere little, if at all, with the efficient working of the gill.

There is not the slightest doubt of the fact of the permanent reversal of the frontal cilia. In all cases stripped filaments were examined at a magnification of 280 or 506 diameters and in many cases the reversal of the current was also demonstrated by carmine particles.

The frontal cilia on the gill filaments of Mytilus are brought to rest at the beginning of their preparatory stroke by increase in osmotic pressure (see Gray, **18**, **19**, p. 54). Presumably owing to increase in osmotic pressure, due to increasing salinity in a preparation by evaporation on a slide, the frontal cilia were found to come to rest at the beginning of their preparatory stroke; it was then seen very clearly that those on either side of the line at which reversal occurs were lying in opposite directions. This would appear to be evidence in favour of the effective stroke being reversed. Gray (**19**, p. 63) remarks that: "It is difficult to imagine how the frontal cilia of *Mytilus*, . . ., could perform any appreciable amount of work during their recovery strokes; but if a cilium is of such a type that there is not much difference between the form of the two strokes it is conceivable that the nett effect of the beat could be reversed

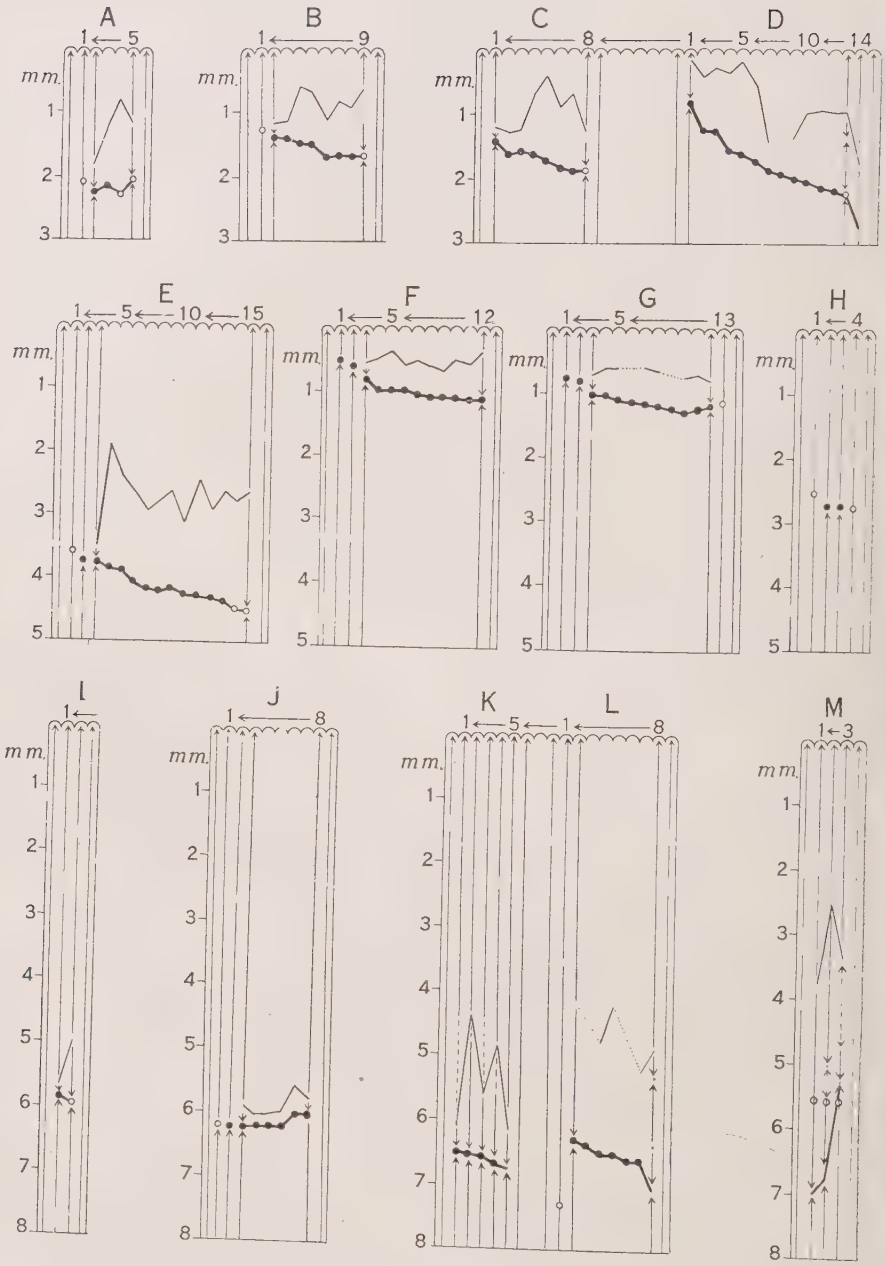

FIG. 6 (description opposite).

by quickening the recovery stroke and slowing the effective stroke as appears to be the case in some protozoa." Parker (**31**, p. 12) suggested that the reversal of Metridium cilia was effected by a system of flexor and extensor elements, placed on the opposite sides of a supporting axis, and his view was elaborated by Williams (**42**).

In *Mytilus edulis*, as in Metridium (**31**, p. 9), the metachronal wave is reversed with the reversal of beat of the frontal cilia.

When the surface of a gill bearing a secondary groove was supplied with carmine particles it was seen that the point of division was by no means always at the same level, or nearly the same level, on adjacent filaments, but as it was thought at first that there might be a simple or direct relation between the influence of the main and the secondary groove, it was decided to strip parts of gills bearing secondary grooves of as many types as possible, to measure the distance from the main groove at which reversal of the beat of the frontals occurred, and to plot the results as a graph.* The results show that if there is a relation between the influence of the main and the secondary groove it is by no means simple : it also appears as though the influence of the secondary groove is exerted as a whole over the adjacent part of the lamella, rather than that the ciliation of each filament is effected only by its own supernumerary groove.

LEGEND FOR FIGURE 6.

FIG. 6.—Graphs showing the relation of the distance of a secondary groove—set directly on the surface of the lamella—from the main food groove, and the points of reversal of the frontal cilia on filaments composing the secondary groove. The direction of beat of the frontal cilia on filaments adjacent to the secondary groove is shown. (Mainly of the gills of *Mytilus edulis*.) The filaments are numbered antero-posteriorly ; arrows between the numbers show the direction of the current in the main groove. Distance from the main groove is shown in mm. Semicircles ◠ denote the main food groove at the free edge of the gill. Filled-in circles ● denote a well-formed secondary groove on a filament. Circles o denote a slight groove or a projection of the frontal surface of a filament. When a projection bears cilia beating anteriorly, the arrow showing the direction of beat of the frontal cilia stops dorsal to the projection and begins again ventral to it ; when the projection is clothed with short frontal cilia beating ventrally, there is no break.

A broken arrow — — —> is used in those instances where the direction of beat of the frontals was somewhat erratic, but the direction of the current was mainly as indicated. A double-headed and broken arrow <— — —> is used when particles at different times passed in opposite directions.

Inner right or left direct or descending lamella = R2 or L2.
Inner right or left reflected or ascending lamella = R1 or L1.
Outer right or left direct or descending lamella = R3 or L3.
Outer right or left reflected or ascending lamella = R4 or L4.

A was on R3, B „ R3, C „ R3, D „ R3 } of one Mytilus.

I was on R1, J „ R1 } of a *Modiolus modiolus*.

E was on L3, F „ L3 } of different specimens of Mytilus.

G „ L3, H „ L3 } of one Mytilus.

K was on R1, L „ R1, M „ R1 } of one Mytilus.

* The measurements were made with a Leitz eye-piece micrometer, No. 2 eye-piece, and a No. 3 objective.

The basis of these observations is given in the following detailed description :—

Ciliation of Filaments Bearing Secondary Grooves Set Directly on the Face of the Lamella.

Graphs of the change of ciliary current on the filaments comprising a series of short secondary grooves, in which the groove is set directly on

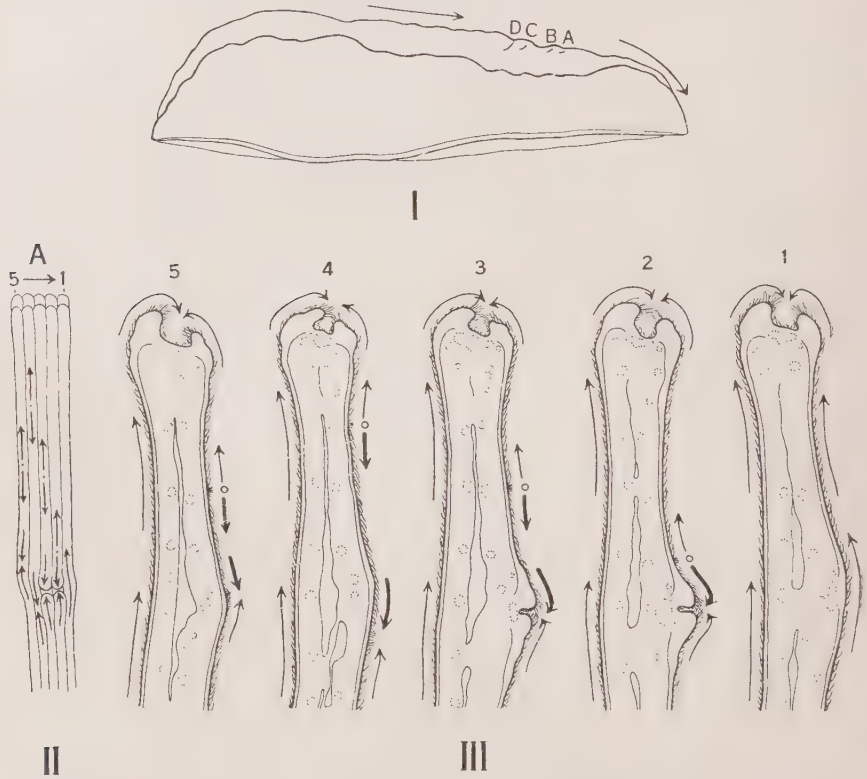

Fig. 7.—I. Sketch of gills of the right side of an infected Mytilus to show the position of the secondary food grooves A–D. The arrows indicate the direction of the current in the main food groves. From life, natural size.

II. Surface view of filaments composing secondary groove A with arrows showing the direction of beat of the frontal cilia. The filaments involved are numbered antero-posteriorly—this order is adhered to in all the figures—and the arrows between the numbers show the direction of the current in the main groove. All figures of surface views, unless otherwise stated, have been constructed from sketches and measurements.

III. Lateral views of single living filaments composing secondary groove A, showing the direction of beat of the frontal cilia. The outline of the filaments, in this and all figures, was traced by the aid of camera lucida. The fine inner line indicates the distribution of the latero-frontal and lateral cilia. The arrows show the direction of beat of the frontal cilia ; heavier arrows are used when the direction is the reverse of normal. I–II × 18¼.

the frontal face of the filament, are shown in Figure 6 (p. 928). The filaments are numbered antero-posteriorly, and where necessary have been so arranged that the first filament is always on the left (in the graphs) from which it follows that the direction of the current in the main and secondary grooves is from right to left.

The graphs in Figure 6, A, B, C and D, are of secondary grooves forming a series on the descending lamella of the right, outer gill of one mussel (Fig. 7, I) where the shortness of the inner gill exposed it to injury by the pea-crab. They were near the main food groove —within 3·0 mm.—and towards the anterior end of the gill.

The secondary groove A (Fig. 7, II), that nearest the anterior end of the

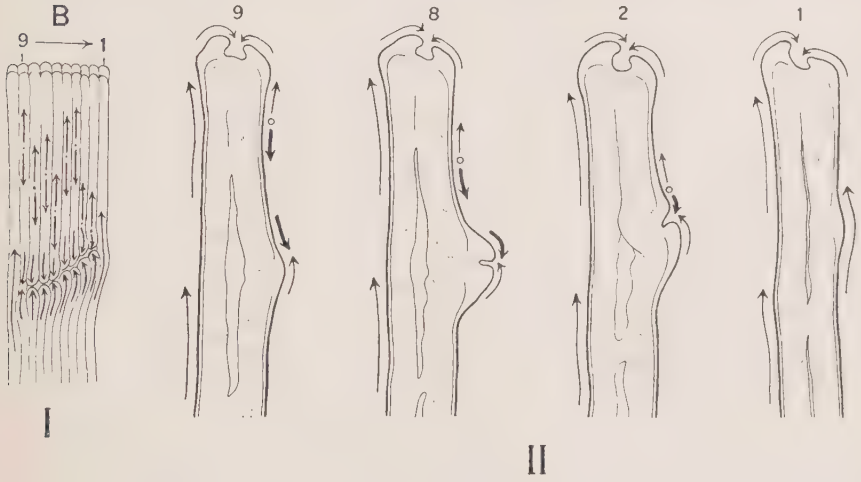

FIG. 8.—I. Surface view of filaments composing the secondary groove B (see Fig. 7, I).
II. Lateral views of representative living filaments. I–II × 18¼.

gill, was composed of only two grooved filaments and all the filaments involved in the abnormality have been drawn (Fig. 7, III). The filament (Fig. 7, III, filament 1) preceding the first grooved filament was nearly normal, there was a break in the rows of latero-frontal and lateral cilia where there was a large elongated ciliated disc, but the length and direction of beat of the frontals was normal. The first grooved filament (Fig. 7, III, filament 2) had a change of ciliary current very near the secondary groove ; in the second grooved filament the change occurred further from the secondary groove. The following filament though practically normal in structure had a change in the direction of the beat of the frontals which was here only 0·82 mm. from the main groove : filament 5 was similar, but the change was 1·2 mm. from the main groove. On both these filaments the cilia at the point of meeting of the currents

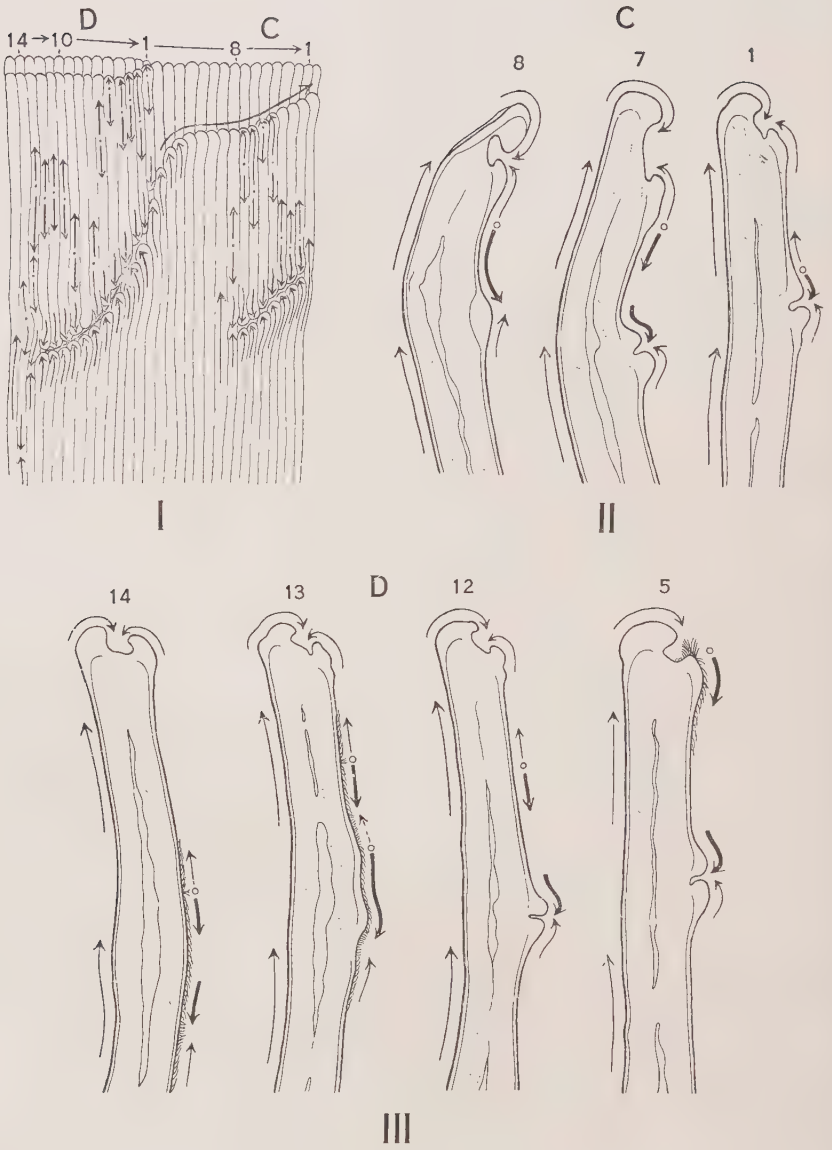

Fig. 9.—Secondary grooves C and D of the gill sketched in Fig. 7, I×18¼.

I. Surface view of filaments composing the secondary grooves. Owing to the accidental crushing of filament 8 of D, the point of reversal of the frontal cilia could not be determined.

II. Lateral views of representative living filaments of secondary groove C.

III. Lateral views of representative living filaments of secondary groove D. The broken arrow denotes a stretch with cilia uneven in appearance, though the current was in the direction indicated. On filament 5 an arrow, which should have pointed into the main grove, has been omitted.

were of the normal length of frontal cilia, but the direction of their beat was towards the anterior end of the gill, that is at right angles to their normal direction. The following filaments were normal in structure and ciliation.

Secondary groove B (Fig. 8, I), next in the series, was composed of seven grooved filaments and sloped slightly towards the main groove anteriorly. The filament (Fig. 8, II, filament 1) preceding the first grooved one was slightly abnormal in structure, but the direction of beat of the frontals was normal. The first and last grooved filaments only are figured (Fig. 8, II, filaments 2 and 8). The frontal surface of the filament following the last grooved one was raised into a slight projection in continuation of the secondary groove, and there was a break in the rows of latero-frontal and lateral cilia ; the reversal of the frontal cilia was only 0·61 mm. from the *main* groove. The next filament was normal both in structure and ciliation.

Secondary grooves C and D (Fig. 9, I) were separated by only seven filaments. In both grooves the slope anteriorly towards the main groove was noticeable, D actually joining the main groove, the sides of which were here very unequal. The filament preceding the first grooved filament of C was normal in structure and ciliation. The point of reversal of the frontals was close to the secondary groove on the first grooved filament (Fig. 9, II) ; it was nearest to the main groove on the fifth filament. Filament 8 following the last grooved filament, although possessing no groove, only a raised area, showed a change in beat of the frontal cilia. The frontal cilia on the projection, where the ciliary currents met, were of normal length but were beating anteriorly. The following filament was normal in structure and ciliation. Filaments from secondary groove D are shown in Figure 9, III. The fact that a reversal of beat occurred on filament 1 (Fig. 9, I), which is unusual, may perhaps be due to the main groove anterior to this filament being very unequally sided, and therefore possibly continuing the influence of the secondary groove. Filament 13 (Fig. 9, III), although grooveless, had two changes in ciliary beat ; the part marked with a broken arrow was rather uneven in beat. Filament 14 was structurally normal, yet had a reversal of the frontal cilia 1·8 mm. from the main groove. On both these filaments the frontal cilia at the meeting of the currents were of normal length, but the direction of their beat was towards the anterior end of the gill. The following filament was normal in structure and ciliation. Filament 8 in groove D could not be measured as it was inadvertently crushed.

Figure 10, I, is a surface view of a secondary groove (E) on the descending lamella of a left outer gill, where it was exposed owing to the shortness of the inner gill. It was between 3·6 mm. and 4·5 mm. from the main groove and sloped slightly ventralwards anteriorly. Figure 6, E (p. 928), is

the graph of this groove and separate filaments are shown in Figure 10, II. The first grooved filament showed no change in beat of the frontals; there was just the break caused by the groove with its long terminal cilia. The filament (Fig. 10, II, filament 14) following the last grooved filament had a distinct projection of its frontal surface, carrying long cilia beating

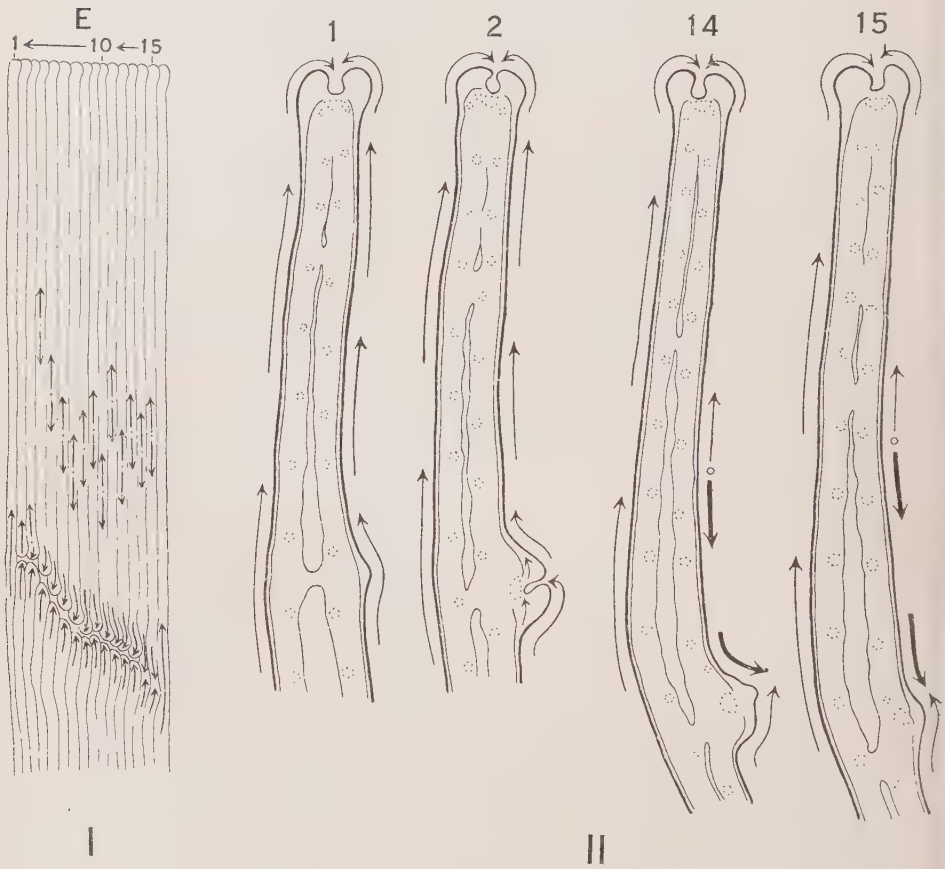

Fig. 10.—I. Surface view of filaments composing a secondary groove (E) on the descending lamella, left outer gill of an infected Mytilus.
II. Lateral views of certain of the living filaments.
I–II × ca. 18¼.

anteriorly, in continuation of the secondary groove, and reversal of ciliary current occurred. Filament 15 had a very slight projection and yet ciliary reversal again occurred: the following one was altogether normal. This secondary groove shows in a definite way the tendency, which is evident from most of the graphs, for the reversal of beat of the frontal cilia to occur nearer the secondary groove at the anterior than at the posterior

end, and that while a grooved filament at the anterior end of a secondary groove may have no reversal of ciliary current, at the opposite end filaments almost normal or normal in structure may yet have ciliary reversal.

Figure 11, I, is the surface view of a short secondary groove (F) on the descending lamella of a left outer gill, exposed by the shortness of the inner gill, and which at the anterior end joined the main groove. No change of beat of the frontal cilia occurred until the third grooved filament and none occurred on that following the last grooved filament (Figs. 6, F, p. 928; 11, I–II); this filament was slightly bent permanently, as were also the next few in the series.

Figure 12, I, is a rough sketch of the two left gills of a mussel with several short secondary grooves on the descending lamella of the outer

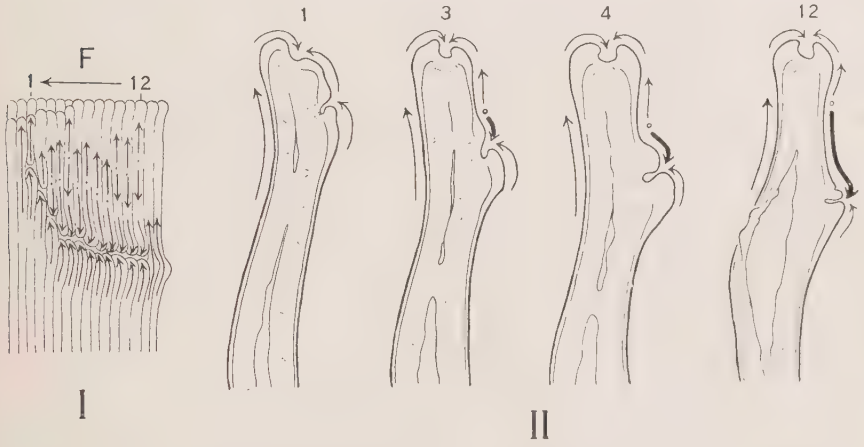

FIG. 11.—I. Surface view of filaments composing a secondary groove (F) on the descending lamella, left outer gill of an infected Mytilus.
II. Lateral views of representative living filaments.
I–II × 18¼.

gill. That nearest the anterior end of the gill was composed of twelve grooved filaments (Figs. 6, G, p. 928; 12, II); it was difficult to strip, as many inter-filamentar connections occurred near the secondary groove, holding several filaments together. Apparently no change occurred—but this is a little doubtful as the first two filaments stuck together—until the third grooved filament (Fig. 12, III, filament 3). The last, though slightly grooved, had no ciliary change, and the cilia clothing the groove were short and were beating ventrally.

On the same gill three tiny incipient grooves occurred in series. That marked H in Figure 12, I, is shown in surface view in Figure 12, IV, and its graph in Figure 6, H (p. 928). The two grooved filaments (one shown in Fig. 12, V) showed no ciliary reversal, only the groove with its long

terminal cilia interrupting the food current. It is interesting to compare this secondary groove with that composed of the same number of grooved filaments of Figures 6, A (p. 928), and 7, I–III (p. 930). The filaments of the remaining two tiny secondary grooves, of about four and six

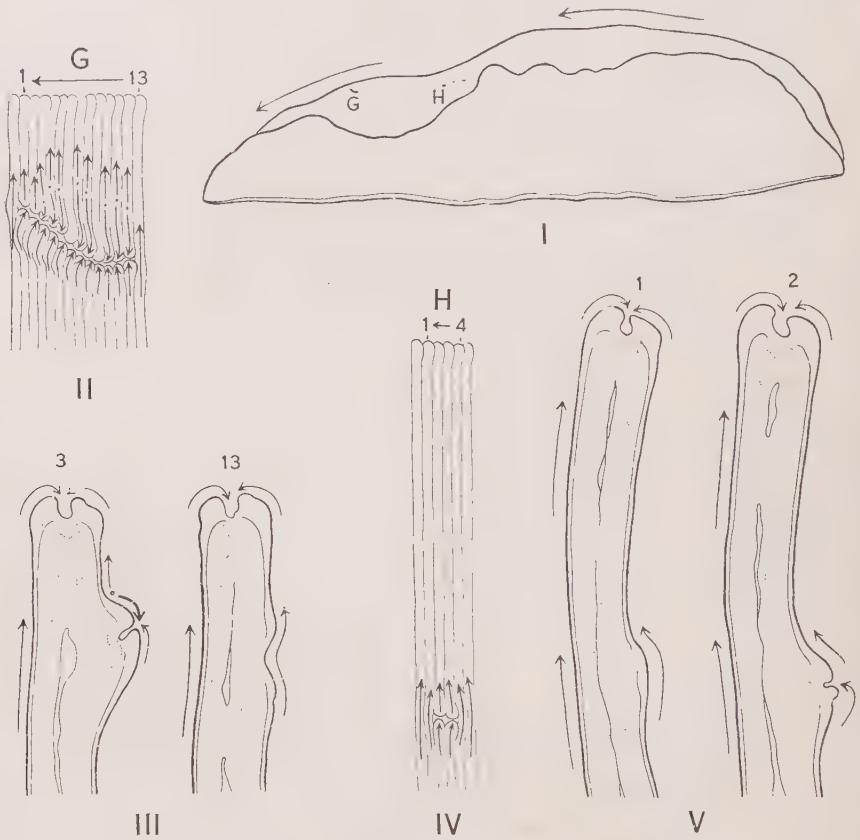

Fig. 12.—I. Sketch of gills of the left side of an infected Mytilus, showing the position of secondary grooves (those investigated are lettered) on the descending lamella of the outer gill where it was exposed owing to the shortness of the inner gill. From life.

II. Surface view of filaments composing secondary groove G. Owing to the fusion of filaments the point of reversal of beat of the frontal cilia on filaments 6 and 9 could not be determined.

III. Lateral views of two living filaments of secondary groove G.

IV. Surface view of filaments composing secondary groove H.

V. Lateral views of two living filaments of secondary groove H.

II–V × 18¼.

filaments respectively, were mostly like the first filament of group H (Fig. 12, V), though some were slightly grooved ; there was no reversal of beat of the frontal cilia.

The gills of a *Modiolus modiolus* containing a pea-crab were found to be

affected; those on the right (Fig. 13, I) more than those on the left. The inner right gill was very short in a small V-shaped area, with several short secondary grooves and some crumpling of the filaments near the

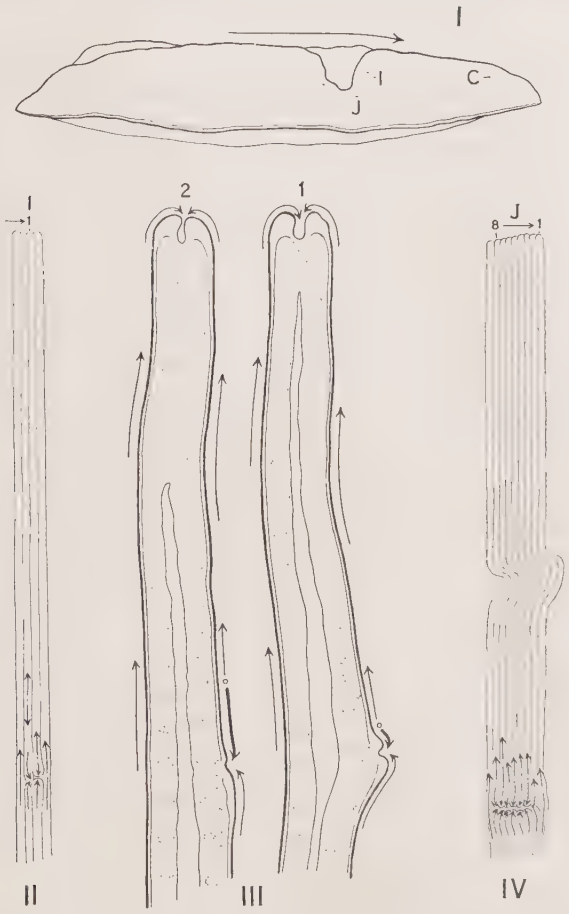

Fig. 13.—I. Sketch of gills of the right side of a specimen of *Modiolus modiolus*, which harboured a large female Pinnotheres, showing shortness of the inner gill in a small V-shaped area and several secondary grooves: those investigated are lettered; I and J are on the ascending lamella of the inner gill, and C indicates the position of a secondary groove on the ascending lamella of the outer gill. Drawn from life. $\times \frac{2}{3}$

II. Surface view of filaments composing secondary groove I.

III. Lateral views of the two filaments composing secondary groove I.

IV. Surface view of filaments composing secondary groove J.

II–IV $\times$ ca. 12.

edge; the crumpling made the filaments very difficult to strip, as where it occurs there is generally considerable fusion of the filaments side by side. (In the normal gill of *Modiolus modiolus*, as in that of *Mytilus*

FIG. 14 (description opposite).

edulis,* there are no organic inter-filamentar connections, only ciliary junctions, and in the former most of the filaments have no inter-lamellar junctions, but an occasional filament has an inter-lamellar septum; the septa vary in height.) In secondary groove I (Figs. 6, I, p. 928; 13, I and II) with only one grooved filament, that preceding the grooved one was normal in structure—except for a few extra ciliated discs—and ciliation. On the grooved filament (Fig. 13, III, filament 1) there was ciliary change very near the secondary groove: filament 2 with only a slight groove, which did not bear long terminal cilia, had reversal about 0·95 mm. from it. The following filament was normal except for a few extra ciliated discs. This secondary groove of one grooved filament would seem to show that the influence of the groove is by no means confined to the filament on which it occurs.

Measurements of the filaments forming the secondary groove J (Fig. 13, I) were difficult to obtain as ventral to the supernumerary groove they were permanently bent. The groove was of the same type as the previous one and the approximate changes in direction of the food current are shown in surface view (Fig. 13, IV) and in the graph (Fig. 6, J, p. 928). No ciliary reversal occurred until the second grooved filament and then was very near the secondary groove. This secondary groove shows the very unusual feature of the occurrence of the point of reversal on the last grooved filament very near (0·25 mm. from) the secondary groove. The frontal cilia on the following filament beat normally. Other secondary grooves—but of another type—on the gills of this specimen of Modiolus will be described later.

The division-line between the cilia beating in opposite directions is mostly definite and clear, with usually a few cilia beating in no definite direction. The three secondary grooves, therefore, on the right inner gill sketched in Figure 14, I, are of special interest in that certain filaments

Legend for Figure 14.

Fig. 14.—I. Sketch of right inner gill of an infected Mytilus, showing the position of three small secondary grooves K, L, and M on the ascending lamella. From life, natural size.

II. Surface view of filaments composing secondary grooves L and K. The broken arrows denote stretches over which the direction of beat of the frontal cilia was somewhat uncertain, but was mainly in the direction indicated. Note the fusion of certain filaments dorsal to the secondary groove L; owing to the fusion the point of reversal of beat of the frontal cilia could not be determined on filaments 3 and 6.

III. Lateral views of three living filaments from secondary groove K. The small area with broken outline near the secondary groove of filament 4 denotes an area of fusion with the next filament.
II–III × 18¼.

* The difference between Modiolus and Mytilus in the shape of the ciliated discs might be noted (cf. Figs. 13 III and 12 III and V) and the possibility of the use of this character in taxonomy.

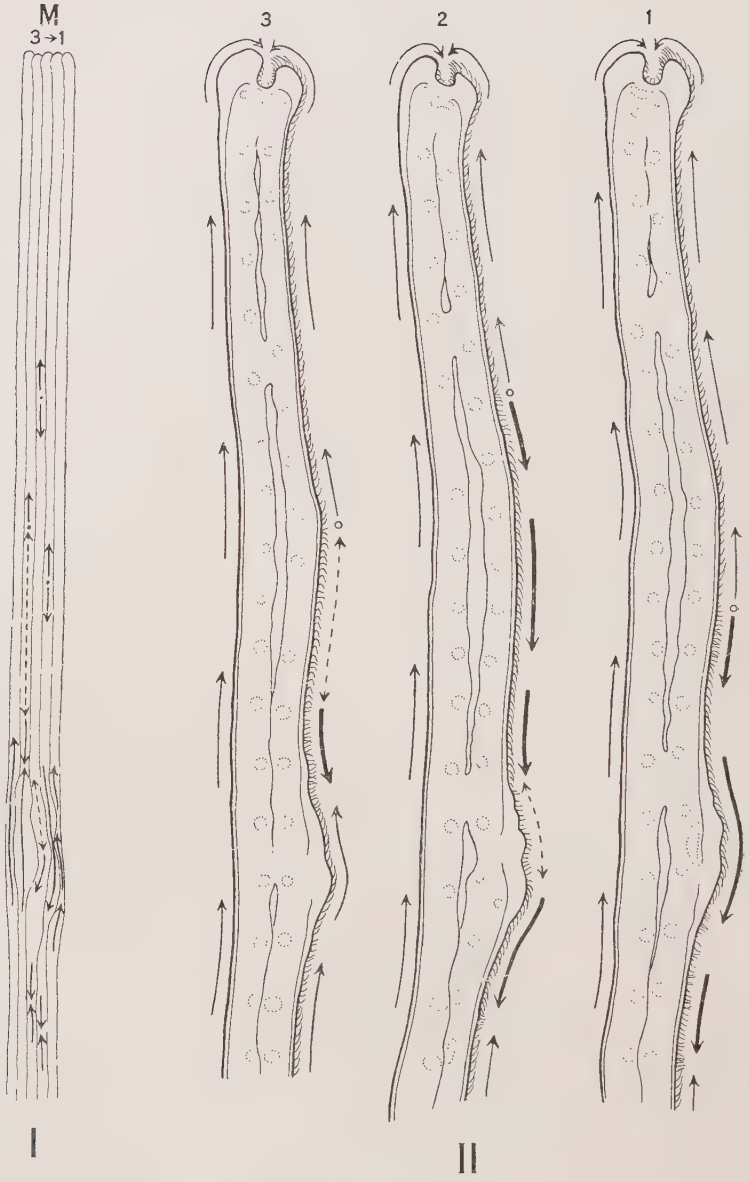

Fig. 15.—I. Surface view of filaments composing the region of enlarged filaments M (see Fig. 14 I). The double-headed arrows indicate stretches over which the current caused by the frontal cilia passed at different times in opposite directions.
II. Lateral views of three living filaments of this region.
I–II × $18\frac{1}{4}$.

from them showed a considerable area over which the frontals appeared to be somewhat uncertain in the direction of their beat. The cilia of these areas had a rough appearance and, when the separate filaments were supplied with powdered carmine, particles were first drawn on to the frontal surface, then flew off, though there was a general tendency for particles to travel in one direction or the other. The supernumerary grooves K and L (Fig. 14, II) which were between 6·0 mm. and 7·0 mm. from the main groove were separated by only four filaments of normal ciliation. The first grooved filament of K, preceded by a normal one, had a stretch of rough-looking cilia between 4·45 mm. and 6·15 mm. from the main groove over which the general direction of the ciliary current was towards the main groove (Fig. 14, III). The second grooved one had a similar stretch, between 4·4 mm. and 4·75 mm. from the main groove, but the direction of particles was chiefly towards the secondary groove. In filament 3 the corresponding area of irregularity was between 4·45 mm. and 5·6 mm. and the direction of the current was chiefly towards the main groove. Filament 4 was slightly grooved; the stretch of irregular cilia was between 4·9 mm. and 5·6 mm. (Fig. 14, III). The following filament (Fig. 14, III, filament 5) was practically normal in structure, though ciliary reversal occurred between 6·15 mm. and 6·75 mm. from the main groove; the cilia over this stretch were somewhat rough in appearance, but the direction of the ciliary current demonstrated by the movement of carmine particles was definitely in the reverse direction to the normal. The filaments in this supernumerary groove stripped singly with ease, those forming groove L, however, stuck badly owing to some fusion just dorsal to the groove (Fig. 14, II) and it was impossible to tell whether there were stretches of uncertain beating. Filament 1 came off singly; there was no reversal of current, the frontal cilia, however, appeared to be absent, or almost so, for a short distance (between 5·55 mm. and 6·75 mm. from the main groove) and particles collected dorsal to this stretch. The next six filaments tore off in two groups of three; the line of division between cilia beating in the normal and in the reversed direction was at 4·2 mm. and 4·8 mm., and 4·2 mm. and 5·2 mm. respectively from the main groove on the outer filaments of the two groups. The last filament, which stripped off singly, is of much interest; although structurally normal two changes of ciliary current occurred (Figs. 6, L, p. 928; 14, II).

The group of filaments M (Fig. 15, I) could not be termed grooved and the elevations of the frontal surfaces did not bear long terminal cilia. In the first two filaments (Fig. 15, II) the area of reversal extended for some short distance dorsal to the abnormal region as though independent of it. On filament 2 for a short distance, between 5·1 and 5·6 mm. from the main groove, there was a tendency for particles to fly off the surface

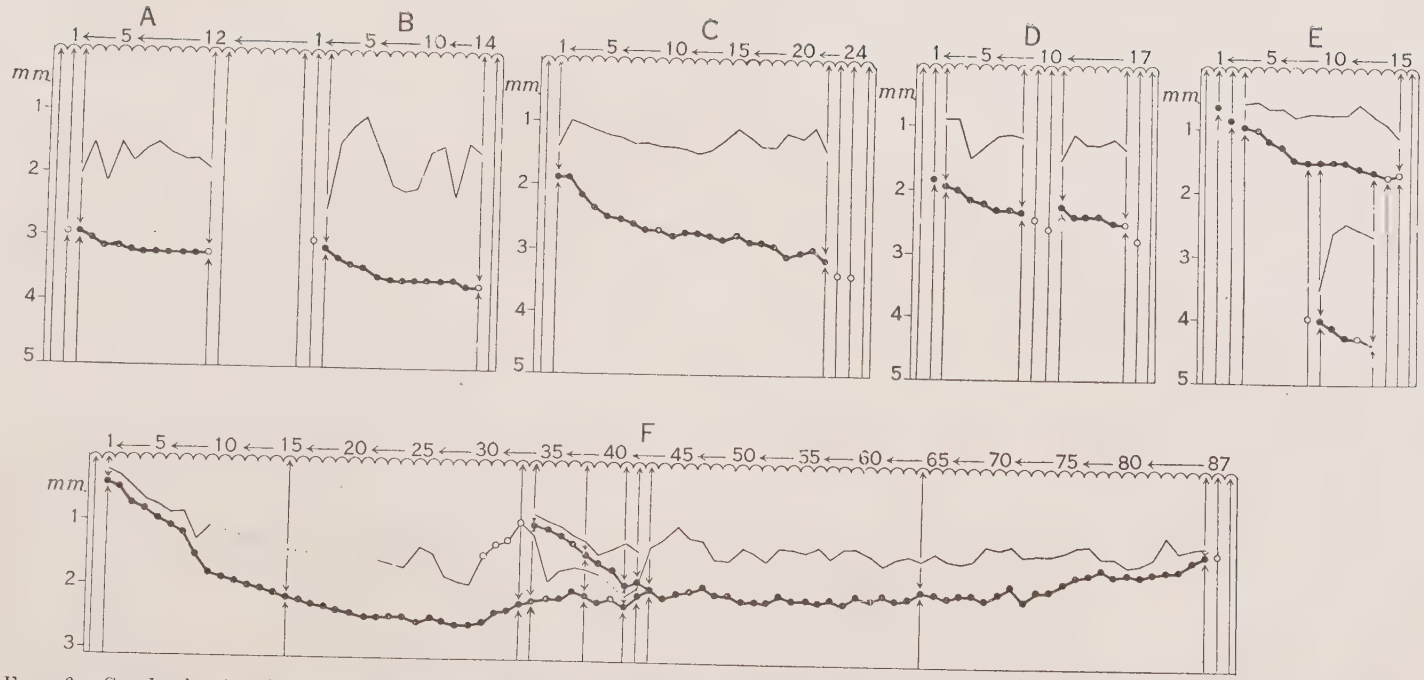

FIG. 16. Graphs showing the relation of the distance of a secondary groove—raised on a slight projection above the surface of the lamella—from the main food groove, and the points of reversal of the frontal cilia on filaments composing the secondary groove. The direction of beat of the frontal cilia on filaments adjacent to the secondary groove is shown. (Mainly of the gills of *Mytilus edulis*.) The signs used are as in Fig. 6, p. 928.

A and B were on L3 of one Mytilus.
C was on R4
D ,, L4 } of one specimen of *Modiolus modiolus*.
E ,, L1
F ,, L3 } of different specimens of Mytilus.

of the filament, but they occasionally passed first in one direction, then in the other. Between 3·4 mm. and 4·75 mm. from the main groove on filament 3 although particles mostly passed dorsally, at times they passed up and down. On all three filaments there were small stretches over which the cilia looked irregular in appearance, but particles passed more or less

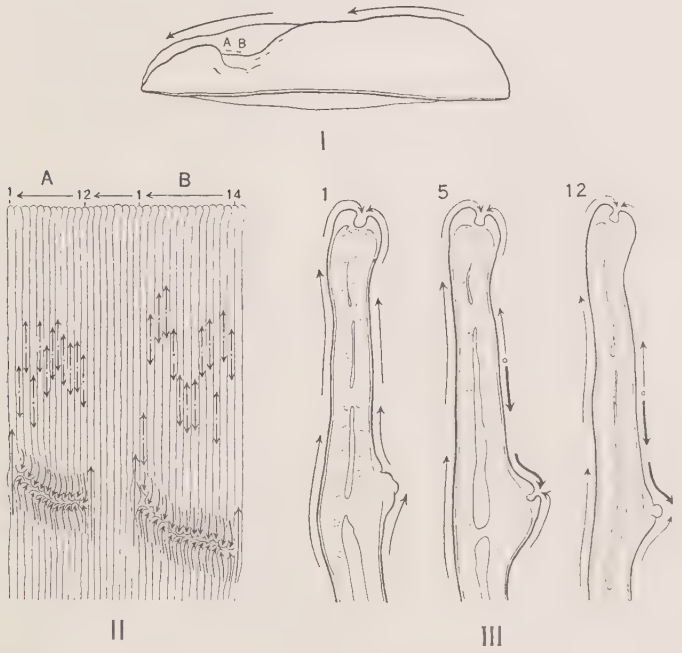

Fig. 17.—I. Sketch of gills of the left side of an infected Mytilus, showing shortness of the inner gill and several secondary food grooves. The two investigated, A and B, are on the descending lamella of the outer gill where it is exposed owing to the shortness of the inner gill. From life, $\times \frac{2}{3}$.

II. Surface view of filaments composing secondary grooves A and B.

III. Lateral views of three living filaments from secondary groove A. II–III $\times$ ca. 12.

definitely in one direction. This apparent uncertainty in the direction of beat of the frontal cilia, over a short length of the filament between two areas in which cilia are definitely beating in opposite directions, is suggestive of the irregularity in beat during ciliary reversal of amphibian embryos described by Twitty (**40**, p. 331), and the impression obtained from the secondary grooves on this gill was that the reversal was unsettled.

Ciliation of Filaments Bearing Secondary Grooves Raised somewhat above the Surface of the Lamella.

In the group of graphs given in Figure 16 have been included those secondary grooves which show slightly more structural alteration of the filaments.

The secondary grooves A and B (Fig. 17, I) on the descending lamella of the left outer gill of a mussel, where it was exposed owing to the

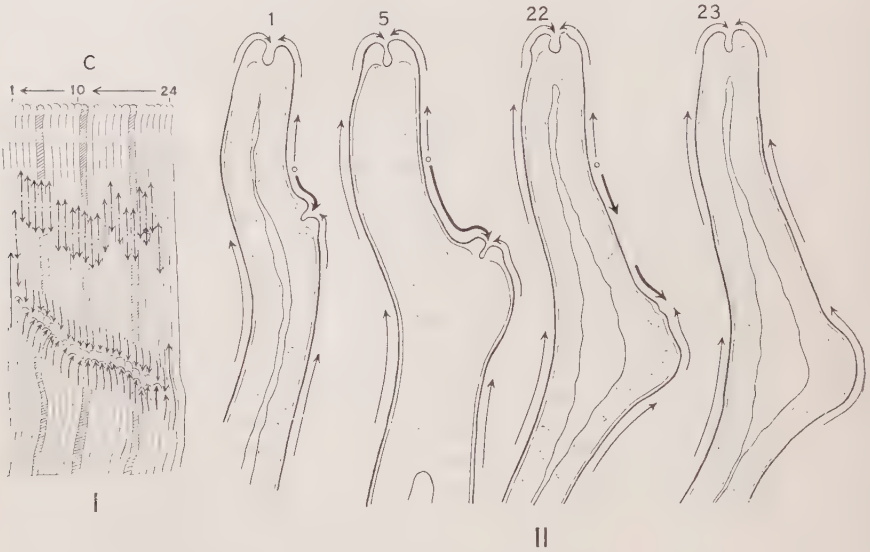

Fig. 18.—*Modiolus modiolus.*

I. Surface view of filaments composing the secondary groove C (see Fig. 13 I, p. 937).
The septate filaments are indicated by shading.

II. Lateral views of representative living filaments.
I–II× ca. 12.

shortness of the inner gill, were separated by only seven normal filaments ; they both showed the characteristic ventral slope anteriorly (Fig. 17, II) and in both the filaments were slightly widened—from frontal to abfrontal surface—beneath the secondary grooves (Fig. 17, III, filament 5). Ciliary reversal occurred on the first grooved filament of A (Fig. 17, I and II, filament 2) ; the preceding one—although having long terminal cilia beating anteriorly—had no reversal (Fig. 17, III, filament 1), on the other hand, reversal occurred on a very similar filament (Fig. 17, III, filament 12) following the last grooved one. The appearance and ciliation of groove B may be gathered from Figures 16 and 17, II.

Two supernumerary grooves of a similar type were present on the gills

of the specimen of Modiolus previously mentioned. The position of groove C on the ascending lamella of the outer right gill is indicated in the sketch in Figure 13, I, p. 937. Groove D was in a similar position on the ascending lamella of the outer left gill. The form of the secondary groove C and the ciliation of the filaments may be gathered from the surface view of the entire groove (Fig. 18, I), the representative separate filaments (Fig. 18, II) and the graph (Fig. 16, c, p. 942). The filament preceding the first grooved one was normal in structure and ciliation.

In groove D ciliary reversal did not occur until the first well-grooved

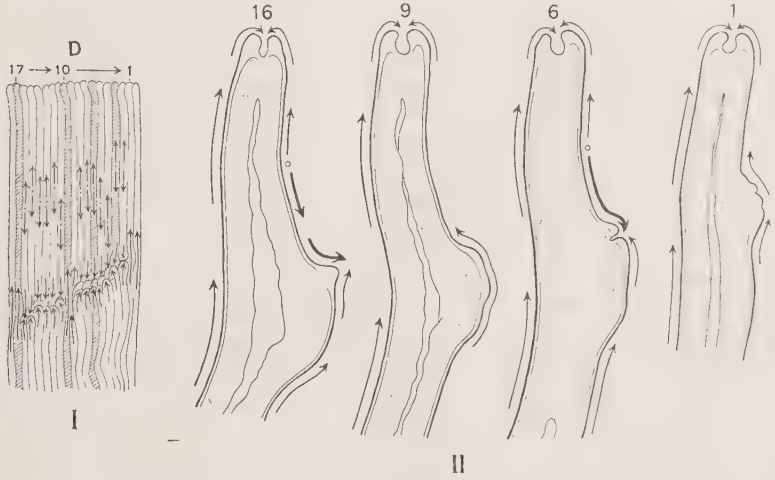

Fig. 19.—*Modiolus modiolus.*

I. Surface view of filaments composing secondary groove D. This was on the ascending lamella of the outer left gill in a similar position to that of secondary groove C on the right gill (see Fig. 13 I, p. 937). The septate filaments are indicated by shading.

II. Lateral views of representative living filaments.

I–II× ca. 12.

filament, although the previous one had long terminal cilia, beating anteriorly, on a projection which was slightly grooved (Fig. 19, II, filament 1). Two grooveless filaments, but with a projection of the frontal surface, occurred between the eighth and eleventh filaments and most unexpectedly there was no reversal of stroke of the cilia on these ; they were very similar in structure and one is shown in Figure 19, II, filament 9. Figures 19, I–II, and 16, D (p. 942), sufficiently indicate the structure and ciliation of this groove.

Gills which have secondary grooves one above the other involving the same filaments would appear to have a possibility of as many changes of ciliary current as there are secondary grooves. In a gill with two secondary grooves one above the other (Figs. 20, I–II ; 16, E, p. 942) reversal occurred

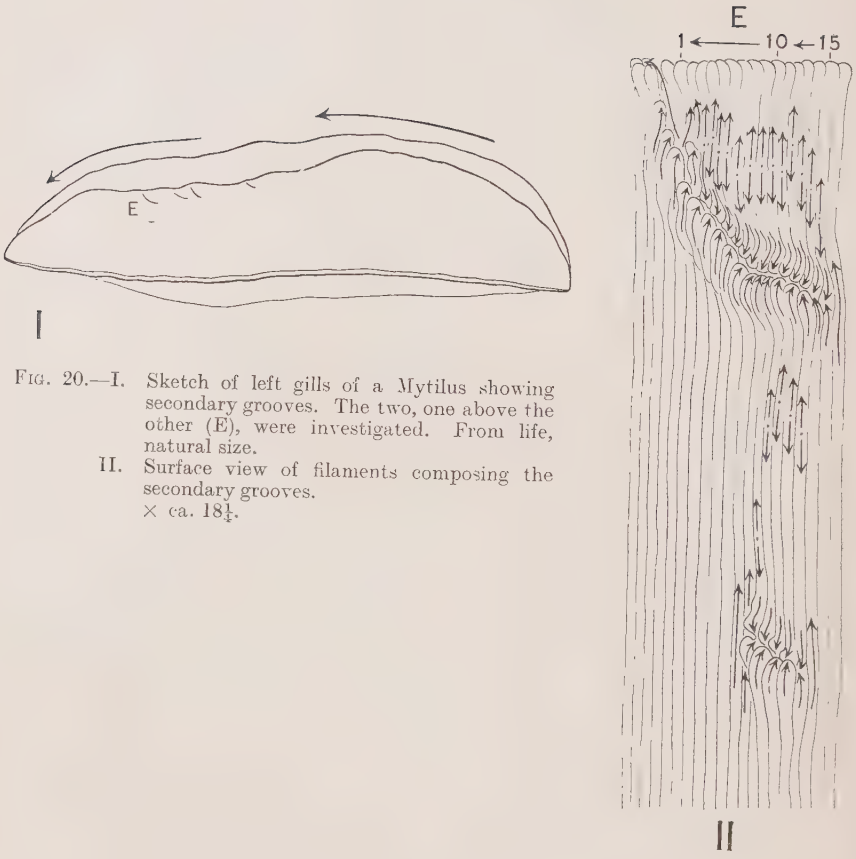

Fig. 20.—I. Sketch of left gills of a Mytilus showing secondary grooves. The two, one above the other (E), were investigated. From life, natural size.
II. Surface view of filaments composing the secondary grooves.
× ca. 18½.

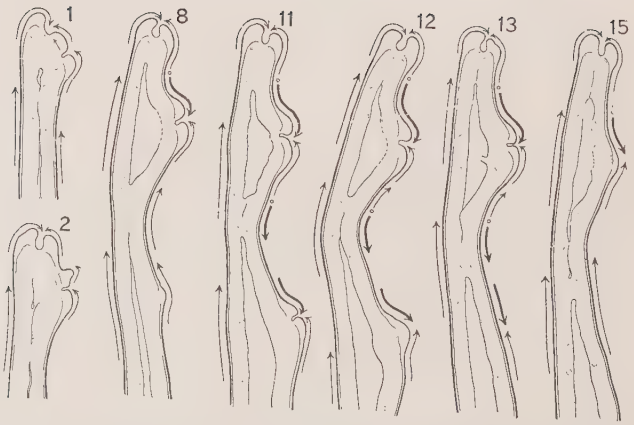

Fig. 21.—Lateral views of certain of the living filaments from the secondary grooves E (see Fig. 20). × ca. 9.

on certain filaments between them, as well as between the main groove and the more ventral secondary groove. The ventral and longer of the two grooves joined the main groove at the anterior end; the tiny—more dorsal one—also sloped in the same direction. In the longer secondary groove no ciliary change occurred until the third grooved filament, while beyond the opposite end of the groove it occurred on filaments 14 and 15, which had merely a projection of the frontal surface (Fig. 21, filament 15). In the tiny more dorsal groove reversal of stroke occurred on the first

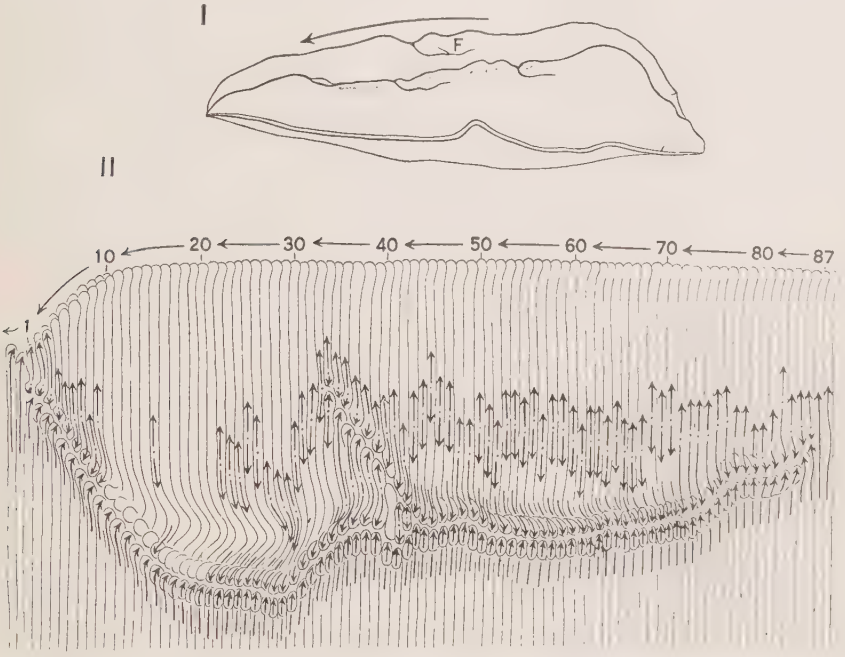

Fig. 22.—I. Sketch of left gills of an infected Mytilus, showing secondary grooves; that marked F was investigated. The stippling indicates abnormally heavy pigmentation. From life, natural size.

II. Surface view of filaments composing the secondary groove. Owing to fusion of certain of the filaments the point of reversal of beat of the frontal cilia could not be determined for filaments 10–14, 16–21, and 40. × ca. 18¼.

grooved filament and at the opposite end occurred not only on filament 12, which had a projection bearing long terminal cilia beating anteriorly, but also on the following one (Fig. 21, filament 13), which was normal so far as this secondary groove was concerned.

A long secondary groove involving 87 filaments and joining the main groove anteriorly had, roughly about the middle of its length, a short secondary groove leading from it (Fig. 22, I–II). The chief secondary groove was borne on a slight projection of the lamella, which over parts

of the groove faced dorsally, and is in this respect rather unusual. The filaments of this secondary groove stripped on the whole easily, but as will be seen from the graph (Fig. 16, F, p. 942) filaments 10 to 14 and 16 to 21 pulled off together ; a few others also gave trouble. It is interesting to compare filaments 33 and 34 (Fig. 23) ; on the former a division of the ciliary current occurs at the slight groove, while on the latter at about the same position two currents meet in the definite groove. The filaments composing this secondary groove showed a tendency for the non-groove-bearing ones (the ascending filaments) to be longer than those (the

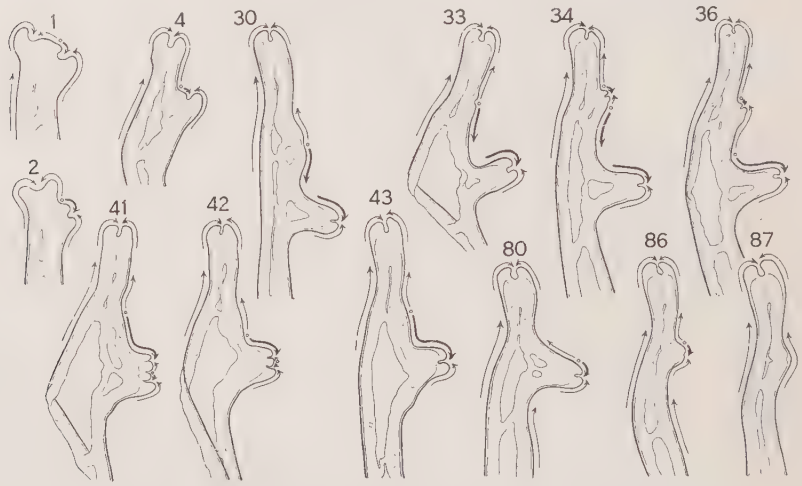

Fig. 23.—Lateral views of representative living filaments of secondary groove F (see Fig. 22). There was a tendency for the non-groove-bearing filament to be longer than that bearing the secondary groove, which made the spreading of the filaments on the slide for examination difficult. × ca. 9.

descending filamen's) bearing a groove and to be bent outwards ; this made the spreading of some of the filaments on a slide for examination a little difficult. Figures 16, F (p. 942) ; 22, I–II ; and 23 sufficiently explain the structure and ciliation of this groove.

Ciliation of Filaments Bearing Secondary Grooves on the Edge of Secondary Folds.

The group of secondary grooves from the gills of one mussel (Fig. 25, I), the ciliation of which is shown graphically in Figure 24, had most of them —with the exception of A, E, and F—in surface view the appearance of deep pockets, but single filaments showed that the appearance was deceptive, the groove being set directly on the surface of the lamella. The structure of some of them would appear to indicate that at one period of

their existence they had been deep pockets (see p. 925). In the secondary groove D from the ascending lamella of the right inner gill of this mussel (Figs. 25 and 24) the pocket must have reached almost to the lower food

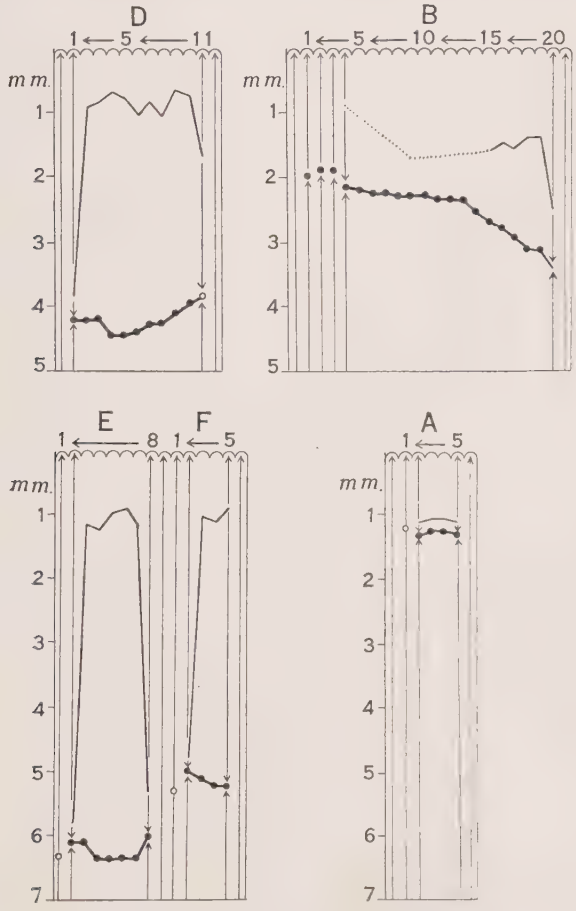

FIG. 24.—Graphs showing the relation of the distance of a secondary groove—on the edge of a secondary fold—from the main food groove on the gill of *Mytilus edulis*, and the points of reversal of the frontal cilia on filaments composing the secondary groove. The direction of beat of the frontal cilia on filaments adjacent to the secondary grooves is shown in most instances. The signs are those used in Fig. 6, p. 928.

A, B, and D are on R1, and E and F on R3 of one Mytilus.

groove. The filament at either end of the groove was of about normal width—from frontal to abfrontal surface—but filament 1 had an extra number of ciliated discs. The filaments towards the middle of the groove, however, such as filament 5 (Fig. 26), showed fairly clearly the probable

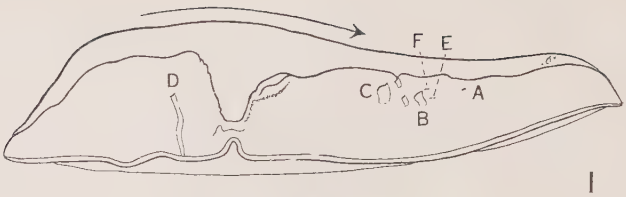

FIG. 25.

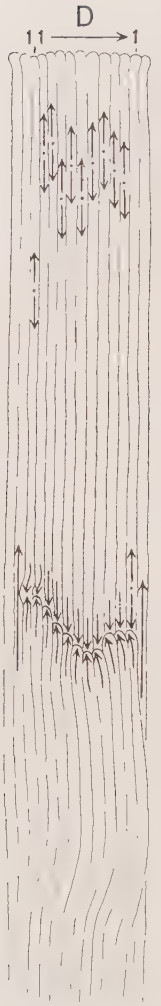

FIG. 25.—I. Sketch of gill of right side from an infected Mytilus, showing shortness of the inner gill and several secondary grooves and folds. Those investigated are lettered; E and F indicates the position of two secondary grooves on the descending lamella of the outer gill. The stippling indicates abnormally heavy pigmentation. Drawn from life, natural size.

II. Surface view of filaments composing secondary groove D. $\times 18\frac{1}{4}$.

FIG. 26.—Lateral views of representative living filaments of secondary groove D (see Fig. 25). $\times$ ca. 9.

previous history of the groove. With the exception of filament 1 the point of ciliary reversal on the filaments composing the secondary groove was much nearer the main than the secondary groove.

Grooves E and F (Figs. 24, p. 949; 25, I, p. 950; 27, I) from the descending lamella of the outer right gill of the same mussel are perhaps of a similar

Fig. 27.—I. Surface view of filaments composing secondary grooves E and F (see Fig. 25 I, p. 950).
II. Lateral views of two living filaments from secondary groove E.
III. Lateral view of living filament from secondary groove F.
I–III× ca. 12.

type to groove D, though fusion of the filaments has gone considerably further, and the irregularity in position and number of the ciliated discs is all that remains to indicate their possible origin. The two grooves were separated by only two filaments of normal ciliation but were not on the same level. Their structure and ciliation is evident from Figure 27, I–III.

It is characteristic of both of them, as of the groove previously described, that except for the first grooved filament in each and the last grooved one of E, the reversal of stroke of the frontals occurred close to the main groove. Filaments 2 and 3 of secondary groove E were fused for a short distance dorsal to the groove (Fig. 27, I).

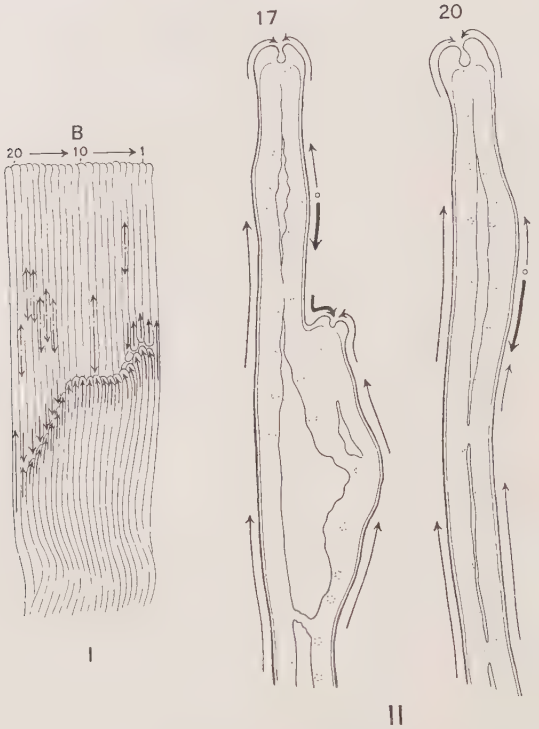

Fig. 28.—I. Surface view of filaments composing secondary groove B (see Fig. 25 I, p. 950).
Owing to the fusion of certain of the filaments the point of reversal of beat of the frontal cilia was not determined for filaments 5–8 and 10–14.
II. Lateral views of two living filaments from secondary groove B.
I–II× ca. 12.

Groove B (Figs. 24, p. 949; 25, I, p. 950; 28) is apparently structurally of a similar type to secondary grooves D, E, and F, but so far as could be judged from very scanty data—the filaments stripped very badly owing to a great deal of fusion occurring—it would not have given the same type of graph as the three previous grooves. Filament 20, following the last grooved one (Fig. 28, II), is interesting in that although structurally normal, ciliary reversal of the frontals occurred.

Groove A (Figs. 24, p. 949; 25, I, p. 950; 29, I–II) was possibly of

the same type structurally as the preceding grooves. Reversal of stroke of the frontal cilia occurred very near the secondary groove on the four filaments composing it, though the point of division on the fourth and fifth filaments is somewhat uncertain as they stuck together.

The 19 or 20 filaments of groove C (Fig. 25, I, p. 950) were of the type drawn in Figure 29, III, and probably the groove was originally a deep pocket. So much fusion occurred between the filaments that no attempt was made to strip the groove systematically. The point of reversal at least

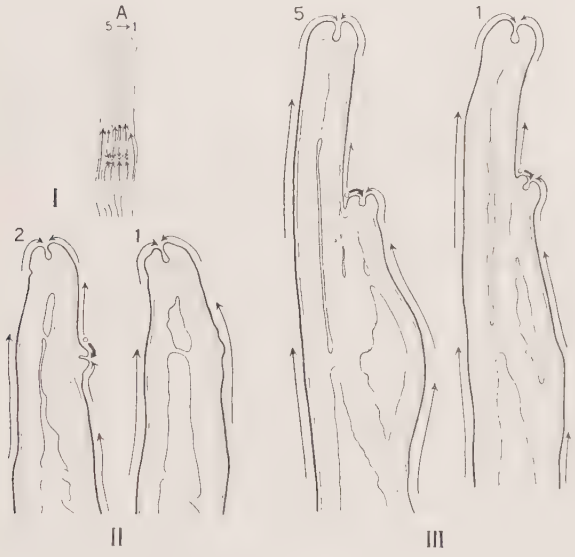

Fig. 29.—I. Surface view of filaments composing secondary groove A (see Fig. 25 I, p. 950).
II. Lateral views of two living filaments of secondary groove A.
III. Lateral views of two living filaments of secondary groove C (see Fig. 25 I).
I–III × ca. 12.

on the first five grooved filaments was exceedingly close to the secondary groove (Fig. 29, III, filaments 1 and 5), so that it is unlikely that it would have given a graph anything approaching the type of D, E, and F.

It is evident from the foregoing observations that the ciliation of filaments bearing secondary grooves, which from the structure of the filaments composing them would appear to have been at one time at the edge of deep pockets, is not always of the striking type shown in the graphs of D, E, and F (Fig. 24, p. 949) in that reversal occurred close to the secondary groove. (Fusion of the ' pocket ' will bring the point of reversal apparently nearer the secondary groove.)

A deep pocket near the posterior end of the right outer gill of another mussel, the groove of which joined the main groove and then diverged, is shown in the rough sketch in Figure 30, I. It is probable that pockets of this type and in this position, that is near the posterior adductor muscle, are not due to injury caused by a pea-crab, even when one is present. Figure 5, I, p. 926, shows a filament from a pocket of similar type and position. The filaments of the secondary fold shown in Figure 30, I, were not systematically stripped; filament A was the first grooved filament,

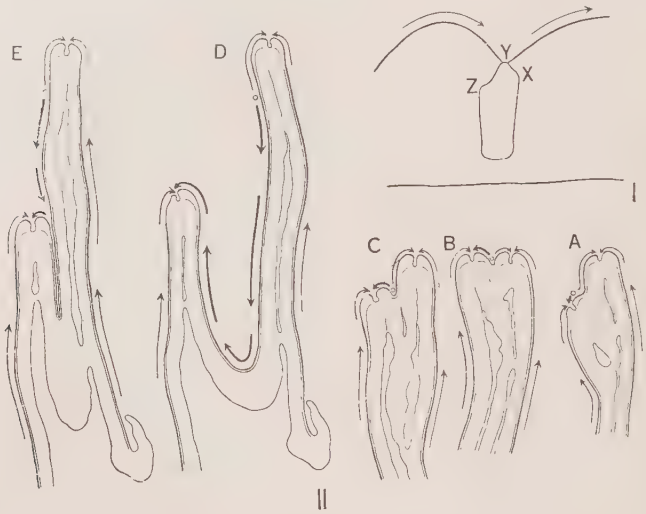

FIG. 30.—I. Rough sketch of a secondary fold or pocket on the descending lamella of the right outer gill of a Mytilus, near the posterior adductor muscle.
II. Lateral views of living filaments from the fold. Filament A was from position X, filament B from about the position Y, and filaments C, D, and E from between Y and Z. × ca. 9.

filament B was from about the position of Y where the secondary groove was on the same level as the main food groove, and filaments C, D, and E were from between Y and Z (Fig. 30, II). Considerable fusion had occurred except between Y and Z, so that the pocket was obliterated as indicated by filaments A, B, C, and E; at some point between Y and Z an open pocket existed as shown by filament D; filament E is from near the posterior edge of the pocket (i.e. near Z). The point of reversal of stroke of the frontals on filaments D and E perhaps lead one to expect that if the filaments had been stripped consecutively the graph would have been of the type of D, E, and F, Figure 24 (p. 949).

Ciliation of Filaments Bearing Secondary Grooves on the same or nearly the same Level as the Main Groove.

The position of a secondary groove of fourteen filaments on the descending lamella of a left inner gill is shown in Figure 31, I. It was so near the main groove that it might be described as a double main groove (Fig. 31, II), and yet ciliary reversal occurred on all the filaments except

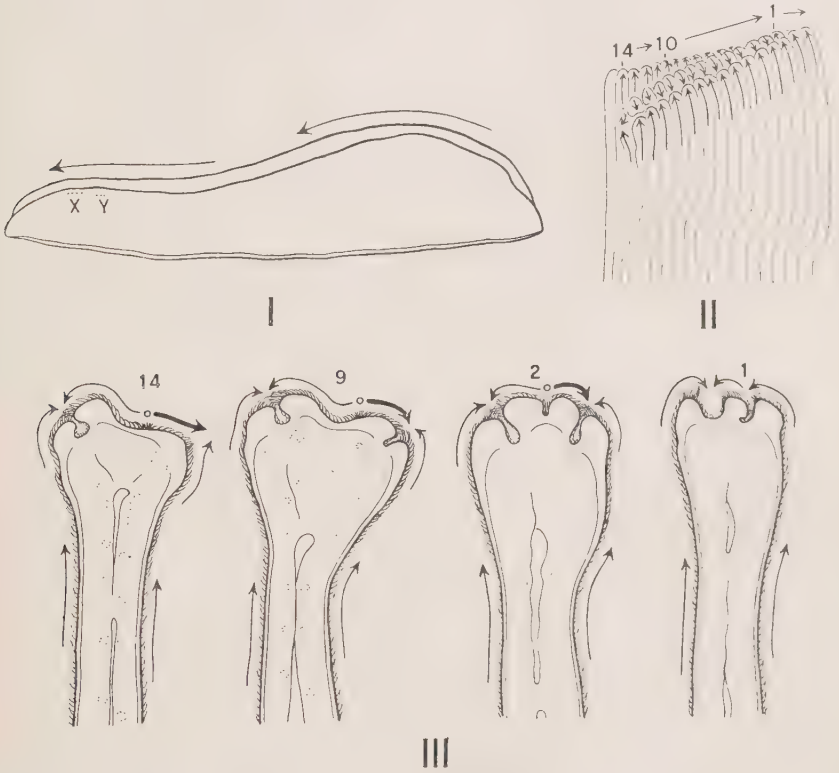

Fig. 31.—I. Sketch of left gills of a specimen of Mytilus: X indicates the position of a secondary groove on the descending lamella of the inner gill, and Y the position of one on the descending lamella of the outer gill. (Secondary groove Y was not investigated.) Drawn from life, natural size.

II. Surface view of living filaments composing secondary groove X. Camera lucida outline.

III. Lateral views of representative living filaments from secondary groove X. II–III × 18¼.

the first; it occurred on the filament (Fig. 31, III, filament 14) following the last grooved filament. On filaments 8 to 12 the point of division between cilia beating in the normal and the reversed direction tended to move slightly towards the secondary groove. Ciliary reversal does not always occur on grooves of this type (see Fig. 35, II, filaments 18–21, p. 963).

Ciliation of Filaments Bearing Secondary Grooves at the Free Edge of the Gill.

As previously mentioned, when a gill is short owing to injury by a large pea-crab the edge is occasionally slightly folded over with some fusion to the lamella (Figs. 4, p. 924 ; 32, I). In such cases very occasionally a secondary groove is present at what is now the free edge of the gill, and a change in the direction of the current caused by reversal of the frontal cilia may occur between the two grooves. Figure 32, II, is the surface view of

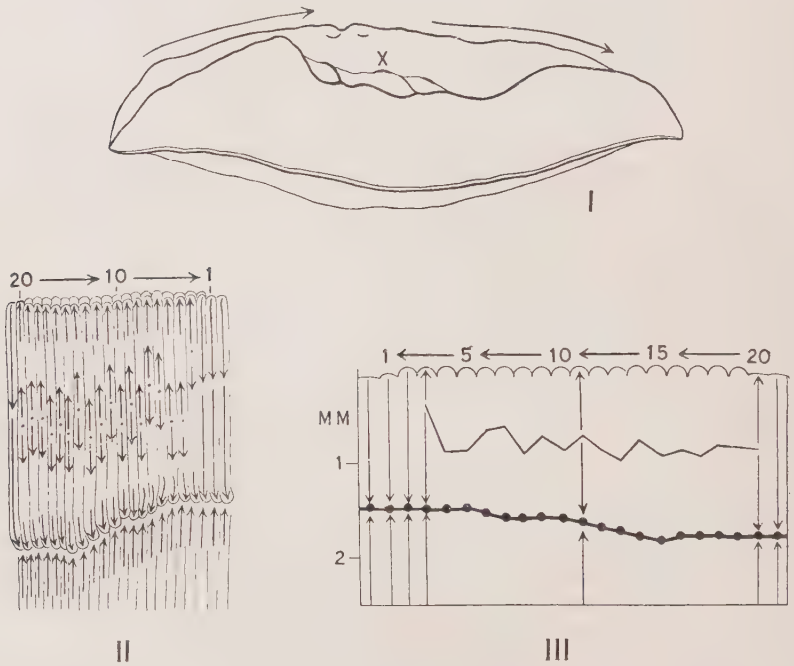

Fig. 32.—I. Sketch of gills of right side of an infected Mytilus, showing shortness of the inner gill and folding over of the free edge with, in certain places, the formation of secondary grooves at what is now the free edge of the gill. The part marked X was investigated. Two secondary grooves are present on the descending lamella of the outer gill. From life, natural size.

II. Surface view of filaments composing the secondary groove X. The secondary groove is at the free edge of the gill, the main groove being folded over. $\times 18\frac{1}{4}$.

III. Graph showing the relation of the distance of a secondary groove X, at the free edge of the gill, from the main groove, which, owing to folding, runs across the surface of the gill, and the points of reversal of the frontal cilia on filaments composing the secondary groove. The direction of beat of the frontal cilia on filaments adjacent to the secondary groove is shown. The main groove in this figure is denoted by filled-in circles, and the secondary groove at the free edge of the gill by semicircles. The arrows at the free edge of the gill show the direction of the food current in the secondary groove and also in the main groove. Distance from the free edge of the gill is marked in mm.

that part of the gill marked X in Figure 32, I, with the change in ciliary beat on the filaments indicated by arrows. From the graph (Fig. 32, III) it will be seen that although the secondary groove is in this instance at the free edge of the gill, there is still a tendency for the change to occur nearer the secondary groove at the anterior than at the posterior end; that while at the posterior end there is change of ciliary current although

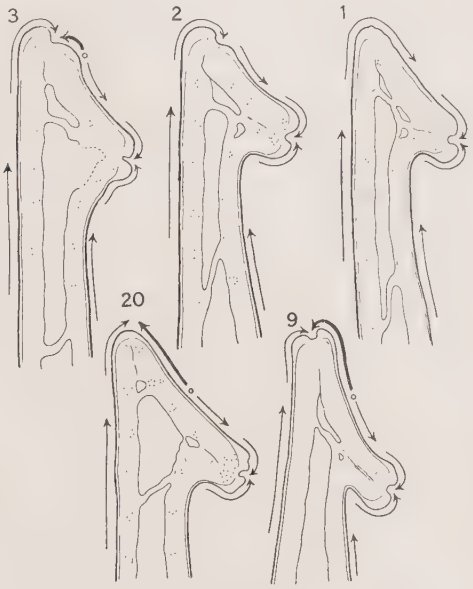

FIG. 33.—Lateral views of representative living filaments from secondary groove X (see Fig. 32). × ca. 12.

there is no groove at the free edge of the gill (filament 20), anteriorly on filament 1, which is enlarged at the edge, and filament 2, which has a shallow groove, there is no change (Fig. 33).

REVIEW OF LITERATURE ON CILIARY REVERSAL.

Known cases of the reversal of ciliary movement in the metazoa are rare, and considerable doubt exists with regard to some at least of those recorded. Purkinje and Valentin in 1835 (**35**) and Engelmann in 1868 (**13**, quoted by Parker, **31**) described reversal of ciliary current on the labial palps of mussels, while Grave (**15**) described it for the labial palps of the oyster; later writers (**1**, p. 129; **2**, p. 233; **22**; **28**, p. 167; **45**, p. 330), however, agree that on the palps of Lamellibranchs there are two permanent ciliated tracts in close proximity which beat in opposite directions and do not reverse their action, muscular movement

determining which set are effective (**1** ; **2** ; **28** ; **41**). Parker (**31**) quotes some case of ciliary reversal in other animals.

Reversal of ciliary current on the lips of the sea anemone *Metridium marginatum* caused by the application of meat extract, potassium ions, etc., but not by mechanical means, has been described in detail by Parker (**30** ; **31**). He states that the reversal is strictly local and lasts only as long as the stimulating substance is present, and that there is no evidence for assuming that it is under any form of nervous control.

Elmhirst (**12**) working on *Actinoloba dianthus* observed that " Longitudinal grooves run down the gullet, and when food is being swallowed the inflow is along the grooves ; conversely a ciliary out-flow runs up the ridges, for example, when a bolus of waste is discharged it is passed out by the cilia on the ridges aided by a certain amount of contraction of the stomodæal wall. At times there is a vortex in the gullet when both sets of cilia are in action at once " (**12**, p. 151).*

In view of this Gray (**19**, p. 60) suggested that " since the oral disc of Metridium is ridged and its muscles are extremely sensitive to mechanical stimulation, one would like to be quite certain that the reversal of the currents observed by Parker is not due to two separate series of cilia which beat in opposite directions on the ridges and in the furrows."

Parker and Marks (**33**) have therefore repeated the experiments with Metridium. They hold that reversal most certainly occurs both of the ridge and groove cilia, though more easily effected in the case of the latter, and that while the cilia of the ridges ordinarily beat outwards and those of the groove beat commonly inwards, there is no evidence of a double system of cilia, one beating constantly outwards and the other constantly inwards on the lips of Metridium.

In a lecture delivered in the summer of 1928, at the Marine Biological Laboratory, Woods Hole, Gray (**19**a, p. 81) mentioned that he had seen " the convincing demonstration by Dr. Parker that a true reversal of the same ciliary current does actually occur " (in Metridium). He said " perhaps it is just possible to imagine that the reversal is due to a change in the ' tone ' of the cilia. For such a suggestion there is some slight experimental evidence."

Torrey (**39**) described reversal of cilia on the lips and œsophagus of *Sargartia davisi*, effected in this instance by mechanical means. Here again the reversal was temporary.

Twitty (**40**) has described the reversal of ciliary action in amphibian embryos, induced by the application of the proper mechanical stimuli.

* Parker (**31**, p. 3) says : " So far as my experience extends, the application of various stimuli to the tentacles has never resulted in a reversal of the effective stroke of their cilia, and the same is true of the siphonoglyphs."

" Those found effective were : intimate contact of the epithelium with a foreign surface, e.g. the floor of a wax or glass dish ; immersion of the embryo in a dense, resistant medium ; contact with the egg membranes in which the embryo develops " (**40**, p. 327). He concluded that the cilia beat in the direction in which they encountered the least resistance. If the stimulus was removed the beat of the cilia returned to the normal after a certain time, which was longer than it had taken to reverse. He remarks that " one often gets the impression that the preference of normal over reversed action is remarkably slight if the conditions are arranged at all suitably " (**40**, p. 329).

The reversal of the beat of the frontal cilia of the gill filaments of *Mytilus edulis* is of a permanent nature. The filaments forming a secondary groove (Fig. 10, p. 934) were stripped one evening and the distance of the point of reversal from the main groove measured. The filaments were carefully kept in order in covered watch glasses and remeasured the next morning. The slight differences in the measurements were such as to be most probably due to error in measuring filaments which are, to a certain extent, contractile. If the ciliary action had been easily reversible, it might have been expected that the dissociation of a filament from its normal position in the gill might have induced a return to the normal direction of beat.

The only attempt to induce a return to the normal direction of beat by cutting off the secondary groove was made on two filaments of the type in Figure 5, I (p. 926), the secondary groove together with the folded part of the filament forming the outer wall of the pocket being cut off. When examined $3\frac{3}{4}$ hours later the points of division, which were 2·6 mm. and 4·1 mm. respectively from the main groove, were in exactly the same position ; when examined again after a further interval of 2 hours there was no change. More experiments of this kind are, however, required.

The possibility must not be overlooked that the ciliated epithelium of the gill filament over which reversal occurs, may have been formed by growth after the production of the secondary groove. If this should occur, the secondary groove would then probably have exerted some influence over the newly formed tissue, causing the cilia as they grew to beat towards it ; in this case it is realized that true ciliary reversal could not then be said to occur. In this connection the gills of the spat of *Mytilus edulis* up to about 3·4 mm. long have been examined and it was found that before the formation of a definite food groove—while there is merely a long tuft of cilia beating anteriorly at the ventral edge of the filaments—the frontal cilia on the very short ascending filaments beat ventrally. The following facts, however, would appear to be against the possibility of the ciliated epithelium over which reversal occurs, having

been formed entirely by new growth after the formation of the secondary groove :

1. The point of ciliary reversal on adjacent filaments is not at the same level ; graphs bring this out clearly.
2. The point of ciliary reversal is at some distance from secondary grooves set directly on the surface of the gill.
3. Ciliary reversal occurs on structurally normal filaments.
4. Little or no reversal of beat of the frontals may occur on all the filaments composing some secondary grooves, even when the filaments are produced into slight folds (Fig. 35, p. 963).

The type of ciliation of filaments forming secondary grooves such as D, E, and F in Figure 24 (p. 949), in which reversal occurs very much nearer the main than the secondary groove —with the exception of the first filament of each and also the last of E—would appear to be a strong indication that cilia, beating originally in the normal direction, had come to reverse the direction of their effective beat.

Fig. 34.

Lateral view of a living filament of a secondary fold on a Mytilus gill. The two food grooves are almost on the same level, and the change of current on the frontal surface of the filaments occurs at the depth of the fold. × ca. 9.

Figures 5, II (p. 926), and 34 show folds or pockets with the change of ciliary beat at the bottom of the pockets ; such might appear to have been formed subsequent to the secondary groove. Unfortunately these pockets were not stripped—a great deal of fusion occurring among the filaments—only one filament from about the middle being examined, so possibly the position of the point of division between cilia beating in the normal and in the reversed direction varied.

Detailed information on the growth (after the early stages studied by Rice, etc.) and the regeneration of the gill of Mytilus, however, will be needed before the origin of the folds or pockets can be decided. Bloomer (**5**), from observations on malformed specimens of *Anodonta cygnea*, concluded that though the animal is able to repair even extensive damage to the mantle-lobes, the gills are not regenerated, the animal being capable of living and thriving with very much aborted gills.

As a rough test as to whether regeneration of the gills of Mytilus occurred, a specimen was wedged open on June 5th, 1929, and several small pieces—more or less triangular in shape—were snipped from the ventral edges of the gills ; it was then allowed to close and put under

circulation in a tank. On September 26th (112 days later) the mussel was opened and the gills examined: they were found to have wedge-shaped pieces—roughly as large or larger than the pieces previously removed—missing from their ventral edges. In all cases, however, where the filaments had been cut across, new food grooves had formed. The mussel when opened was in very good condition, that is well fished, so that the non-occurrence of regeneration—with the exception of the food groove—could not be attributed to lack of food.

The result in this case may be regarded as an indication that a food groove only is regenerated after injury, at least at the free edge of the gills; conditions governing growth and regeneration on the surface of the gills may, however, be different from those governing growth at the free edges.

Mussels are not infrequently found having gills with very jagged ventral edges.

One of the pieces cut from the gill had caused a state of affairs of some interest. It was in the shape of a long, narrow wedge, slanting very much antero-posteriorly, in such a way that the ventral ends of 13 filaments—forming a small triangular area -had been severed from organic connection with the gill, and apparently were only connected with each other by ciliary junctions, while the longest piece, forming the base of the triangle, was connected in the same manner with a normal filament. There is the possibility that organic inter-filamentar junctions may have been formed owing to compression by the cutting, but any such were not obvious and it is improbable that all filaments would have been so connected. The gill was preserved without pulling the filaments apart.

The dorsal cut ends of these apparently organically isolated pieces of filaments had in some cases rounded off and in others had formed a rough food groove, but all, except the shortest and the longest, had developed long terminal cilia, beating anteriorly, at the cut ends. Owing to the triangular shape of the piece the direction of the current produced by these was roughly anterior and dorsal, and met the current from the posterior part of the gill at the depth of the cut. There appeared to be no reversal of the ciliary current on these pieces of filaments, with the possible exception of some very tiny areas near the new groove on some of them, over which particles seemed to pass towards the groove; the current, however, may have been caused by the newly formed terminal cilia.

The 13 pieces of filaments after 112 days were slightly swollen, as filaments of a gill cut from a mussel will generally become after several days in a finger-bowl of sea-water; the cilia, however, were beating vigorously. These, most probably, organically isolated pieces of filaments had therefore in some cases at least regenerated a food groove by the transformation of material, and all with the exception of the shortest and

the longest had grown long terminal cilia beating in the same direction as those along the main food groove at the ventral edge of the gill. It is hoped to repeat this experiment.

Discussion on the Possible Causes of Ciliary Reversal.

From an analysis of the graphs of various secondary grooves it is evident that there is a distinct tendency for the change of ciliary current to occur nearer to the secondary groove at the anterior end of the groove than at the posterior end. In fact at the anterior end a filament with a definite groove may show little or no reversal, particles dorsal to the groove passing into and along it, but all particles ventral to it passing into the main groove. On the other hand, not only is the point of change generally further from the secondary groove at the posterior end, but there may be reversal of cilia on a filament with only a slight projection of the frontal surface, and in a very few instances on a filament perfectly normal except for the ciliary reversal. Cases such as shown in Figure 6, D and L (p. 928), where there are two changes of ciliary current on structurally almost normal filaments are very difficult of explanation, the only possibility seeming to be that the direction of beat is unsettled.

It would appear that the ciliary change is due to the effect of the secondary groove as a whole, and that the change does not occur on a filament entirely independent of its neighbours.

Lillie (**24**, p. 428) has explained the waves of co-ordinated beating such as occur in the rows of swimming plates of ctenophores in the following way: "... increased ciliary activity in one area excites adjoining areas to increased activity, so that a certain synchrony tends to be preserved between neighbouring cells. If ciliary activity, like other forms of contractility, is due to variations of electrical polarization at the surfaces of the contractile elements, an action-current must accompany each ciliary stroke, and its stimulating influence will be transmitted through the medium for some distance."

Wyman (**44**, p. 558) working on the gills of Unio observed that: "The transmission through the gill of the effects of warmth applied locally is apparent through increased rate of ciliary beat on adjacent gill tissue in all directions from the region of application." He offers an explanation similar to that of Lillie that: "The phenomenon might be explained by the stimulating effect of the action-current of the directly excited cilia on the neighbouring relatively quiet cilia," but remarks that "such an explanation, though in accord with the work on Unio, is inconsistent with certain of the observations of Kraft (**23**) on the tissue from the frog's pharynx."

Whether there is any possibility of an action-current being sufficiently

strong to reverse the beat of the frontal cilia of Mytilus, experiments will be necessary to determine.

The suggestion is also very tentatively made that the reversal of beat may be due to the mechanical resistance of a water current, set up by the

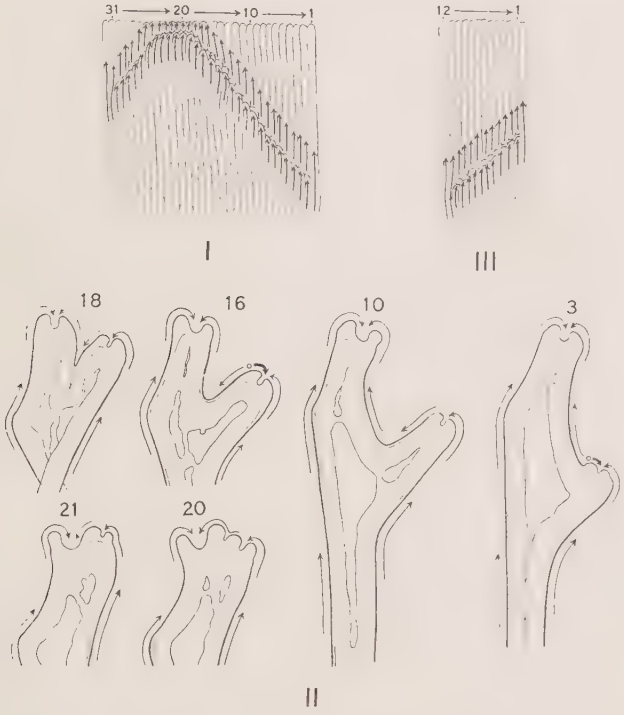

Fig. 35.—I. Surface view of filaments (Mytilus gill) composing a secondary groove which joined the main groove and then diverged. Little or no change of current occurred on the filaments.

II. Lateral views of representative living filaments from the groove. In filaments 3 and 10 especially, the outward bend—due to its greater length—of the non-groove-bearing filament is noticeable. In filament 18 the broken outline indicates an area of fusion with the next filament.

III. Surface view of filaments composing another secondary groove from the gill of the same mussel. They were of the type of filaments 3 and 10 of II, and little or no reversal of beat of the frontals occurred.

I–III× ca. 12.

long terminal cilia beating along the secondary groove. This suggestion would seem to account for the fact mentioned above that the change is generally closer to the secondary groove at the anterior than at the posterior end of the groove. Examination for a current set up by the

terminal cilia of the secondary groove, by means of powdered carmine, however, only revealed what appeared to be a weak one over the surface of the gill at the level of the secondary groove. This current was drawn into the groove at an acute angle.

That in some instances the change is very near the main groove indicating that the secondary groove appears to have more influence than the former, may perhaps be due to the fact that the secondary groove is on the surface of the gill and therefore any current set up by its long cilia would have more effect over the surface of the gill than would the main groove at its free edge.

One would expect the change in direction of beat to be a gradual and increasing one, and secondary grooves which have caused little or no change in direction of beat of the frontal cilia of the filaments of which they are composed, could be explained by assuming their recent formation. Examples of such grooves are those in Figure 35. After filament 18 of that in Figure 35, I, the secondary groove was almost on the same level as that of the main one for several filaments, then gradually diverged from it until at the 31st and last filament it was 0·8 mm. from the main groove. The filaments composing the secondary groove shown in Figure 35, III, were very similar in structure to filaments 3 and 10 in Figure 35, II. Particles on the gill dorsal to these secondary grooves passed into and along them, while those drawn on to the surface of the gill ventral to them passed almost entirely into the main groove.

The fact that experiments in transplanting pieces of ciliated epithelium from the roof of the mouth of the adult frog (**6** ; **25**) and from the trachea of the dog and the cat (**21**), reversing them in direction, have shown that the cilia on the transplanted pieces do not come to beat in the direction of the surrounding cilia of the host, the water current set up by them apparently having no effect, would seem to vitiate the possibility of the reversal of the frontal cilia of the gill filaments of Mytilus being due to the resistance set up by a water current. In Mytilus, however, the long terminal cilia of the grooves are considerably longer than the frontals, and might be expected to produce a stronger current, more likely to overcome the resistance of the frontal cilia.

Nervous control of ciliary action, chiefly of locomotor cilia, is known in certain forms (**8** ; **9** ; **10** ; **11** ; **26**) and Merton (**27**) contends "that reversal is always a manifestation of such regulation. He would thus class reversal as one of the spontaneous or voluntary responses of the organism" (quoted from Twitty, **40**, p. 326). Nervous control of the branchial cilia is said to occur in *Doliolum mülleri* (**14**). Grave and Schmitt (**16**) have described the presence of nerve-like structures lying immediately beneath, and parallel to the ciliated cells of the latero-frontal epithelium of Lampsilis, and in the epithelium itself a series of inter- and intra-

cellular fibrils with a suggested co-ordinating function. Bhatia (**4**) from an investigation of the latero-frontal cells of Mytilus has pointed out that in all probability the inter-cellular fibrils are cell walls, which, owing to the plane of the sections, are not seen in their entirety. Up to the present it has been found impossible to detect the operation of nervous elements in the epithelium or in the cells themselves of the gills of Mytilus (see Gray, **18**, p. 108); it would therefore appear to be unlikely that reversal of beat of the frontal cilia is due to nervous control.*

The work was done at Plymouth while holding a Miss Busk Research Studentship, 1927–28, and an Amy, Lady Tate Scholarship, 1928–29, of Bedford College. I wish to thank the College authorities for allowing me to continue to work at the Marine Station; the London University for granting me the use of their table; and the Director and Council of the Marine Biological Association for facilities. My thanks are also due to Miss Sexton for bringing to my notice an important reference to the literature, and to Mr. A. J. Smith for the photograph in Figure 3. And, finally I should like to express my deep indebtedness to Prof. J. H. Orton for the interest he has taken in the work, and for his advice and criticisms.

SUMMARY.

Permanent reversal of the frontal cilia on the gill filaments of *Mytilus edulis* has been found to occur naturally in the majority of cases where secondary or supernumerary food grooves are present on the gill. Such secondary grooves possibly arise as the result of injury; in some localities they are strongly correlated with the presence of a large female *Pinnotheres pisum* in the mussel. In these cases there is strong presumptive evidence that the secondary grooves are caused by mechanical injury from the claws of the crab. Considerable growth of inter-filamentar junctions, together with fusion of the filaments side by side, is common in secondary grooves and folds, and is especially marked in folds the filaments of which are somewhat askew.

The cavity of a fold or pocket practically always faces ventrally, and there is a definite tendency for the secondary grooves to slope ventrally and anteriorly.

The cavity of pockets would appear to be sometimes obliterated by

* While this account was in the press an interesting paper by S. B. Setna on "The Neuro-muscular mechanism of the gill of Pecten" was published in the *Q.J.M.S.*, Vol. 73, pp. 365–391, February, 1930. In describing the innervation of the gill and in connection with an unsuccessful attempt to determine the function of the subsidiary branchial nerve, he remarks: "While its sensory function cannot be denied, another possibility is that the cilia on the palps and the gills may be under nervous control. . . . On cutting the subsidiary branchial nerve, however, there is no evidence of reversal either on the gills or on the palps, nor does mechanical stimulation alter the direction of the ciliary stroke." (p. 382).

the concrescence of the filaments forming them; illustrations of the stages in the possible process are given.

Generally one or two filaments at either end of a secondary groove are raised into a projection in continuation of the groove; such projections may occasionally bear long terminal cilia beating anteriorly (i.e. at right angles to the normal direction of the frontal cilia), or may be covered with frontals of normal length, in some instances beating anteriorly and in others beating ventrally, according as to whether reversal does or does not occur on the filaments.

About 27 secondary grooves have been investigated, and it has been found that the reversal of beat of the frontal cilia of the gill filaments occurs over a variable distance between the secondary and main grooves. Particles drawn on to that part of the gill over which cilia beat in a reversed direction are carried dorsally into the secondary groove and along it until they reach a filament with normal ciliation, along which they are passed into the main groove. The direction of the current is the same in the secondary as in the main food groove, that is towards the mouth.

The metachronal wave is reversed with the reversal of stroke of the frontal cilia.

The point of division between cilia beating in the normal and in the reversed direction is not at the same level on adjacent filaments forming a secondary groove. Reversal is usually nearer the secondary groove at the anterior than at the posterior end of the secondary groove, and ciliary reversal may even occur on the following one or two ungrooved—and very rarely even on perfectly normal—filaments at the posterior end of the secondary groove; the graphs show this clearly. From a consideration of the graphs it seems apparent that the influence of the secondary groove is exerted as a whole over the adjacent part of the lamella and each filament is not influenced by its own groove independent of its neighbour.

The ciliation of filaments composing certain secondary grooves, which from their structure would appear to have been originally at the edge of deep pockets, is of interest in that the point of division between cilia beating in the normal and in the reversed direction is much nearer the main than the secondary groove, with the exception of certain few filaments. This type of ciliation would appear to be a strong indication that cilia beating originally in the normal direction had come to reverse the direction of their effective beat.

The possibility is not overlooked that the epithelium bearing cilia beating in the reversed direction may be partly formed anew after the production of the secondary groove, whence the probability would be that the influence of the secondary groove may have caused cilia from the very beginning of their appearance to beat towards it (i.e. in the

reversed direction to the normal), in which case there would have been no true reversal.

Possible causes of the ciliary reversal in Mytilus are discussed. A little experimental work has been attempted, and it is suggested that a full explanation of the phenomena observed must await the result of an extended series of experiments.

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Abstracts of Memoirs.

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY.

Structure of Pearls.

By C. Amirthalingam.

Nature, *No.* 3091, *Vol.* 123, 1929, *p.* 129.

Pearls from the tissues of a Pinna showed that the conchyolin layers may be arranged radially as found in Pinna shells or concentrically round the nucleus as in *Ostrea edulis* pearls ; in two cases, however, an alveolar layer was found round the nucleus with concentric layers on the outside. The nuclei of twenty-nine pearls out of thirty-two, were found to be conchyolin ; this observation supports the view that the origin of pearls is due to abnormal secretion of the epidermis.

C. A.

The Integration of Light by Photo-electrolysis.

By W. R. G. Atkins and H. H. Poole.

Sci. Proc. R. Dub. Soc., 1929, *Vol.* 19, *pp.* 159–164.

It is possible to use a vacuum photo-electric cell for the integration of light. A Burt sodium cell gave 1·15 microamperes per 1000 metre-candles. On a bright November afternoon the production of alkali by the photo-electric current was observed in a dilute bicarbonate solution within 10 seconds, using brom thymol blue as indicator. The current may also be used for the deposition of copper. An average winter day should give about 0·13 mg. with the photometer horizontal ; in summer nearly 1 mg. might be expected.

W. R. G. A.

The Photo-electric Measurement of the Illumination in Buildings.

By W. R. G. Atkins and H. H. Poole.

Sci. Proc. R. Dub. Soc., 1929, *Vol.* 19, *pp.* 173–187.

By the use of vacuum sodium photo-electric cells of the Burt type, together with suitable portable galvanometers, simultaneous measurements were made of the illumination in the open and in buildings ; the ratio expressed as a percentage, the daylight factor, is a useful index

of the illumination inside. This applies to diffuse skylight. A correction must be applied when the sun is shining, the illumination in the shade being multiplied by a factor β, which denotes the ratio of the reading of the photometer in the open site, to that obtained when the direct sunlight has been screened off. In an old church the daylight factor varied from 0·02 to 0·86 per cent for vertical illumination with the blue sensitive sodium cell. In a dwelling-house the factor immediately inside large windows was 7 per cent. The value in a well-lighted room is under 1 per cent. From this it follows that it is uneconomical to fit glass transparent to ultra-violet light in windows other than those that receive direct sunlight.

W. R. G. A.

Photo-electric Measurements of Illumination in Relation to Plant Distribution. Part II. Measurements with Portable Galvanometers.

By W. R. G. Atkins and H. H. Poole.

Sci. Proc. R. Dub. Soc., 1929, *Vol.* 19, *pp.* 295–309.

By the use of Burt cells, robust Onwood micro-ammeters and suitable shunts simultaneous measurements were made of the vertical illumination in the open and in shaded sites. The photometer windows, as before, were sheets of double surface-flashed opalised glass. Large obliquity factors are thus avoided. The results obtained for measurements of the daylight factor agreed well with those determined by the rate of decomposition of uranyl oxalate solutions in quartz tubes. The daylight factor is not a constant, but varies somewhat according to the distribution of the illumination in the absence of sunlight. The factor is sufficiently constant to be a useful index of the light received at any spot. Data are presented showing the behaviour of certain plants growing in varying degrees of shade. In the deepest shade measured, daylight factor 1·3 per cent, only straggling branches of *Hedera helix* were found.

W. R. G. A.

The Uranyl Oxalate Method of Daylight Photometry and its Photo-electric Standardization.

By W. R. G. Atkins and H. H. Poole.

Sci. Proc. R. Dub. Soc., 1929, *Vol.* 19, *pp.* 321–339.

The rate of decomposition of uranyl oxalate was compared with the reading of a potassium vacuum photo-electric cell which had been standardised by means of an open carbon arc. After making due allowance for the difference in the absorbing surfaces it was found that the

rate of decomposition of the standard solution, in quartz tubes, was 0·225 c.c. per hour per thousand metre-candles. Tubes of Monax glass required 1·14 times as long an exposure to produce the same result. This should not prevent their use for ecological work.

Measurements of the mean horizontal illumination were made at sea over two complete days by means of tubes suspended in the rigging, the average for the period from sunrise to sunset being 25,800 metre-candles on August 17 and 23,600 m.c. on September 18th, 1928.

The usual practice of exposing photo-sensitive liquids in vertical tubes measures the mean horizontal illumination. Exposure in a spherical flask measures the total illumination. This is desirable for some purposes.

W. R. G. A.

The Photo-chemical and Photo-electric Measurement of the Radiation from a Mercury Vapour Lamp.

By W. R. G. Atkins and H. H. Poole.

Sci. Proc. R. Dub. Soc., 1929, *Vol.* 19, *pp.* 355–361.

The uranyl oxalate method was used to study the rate of deterioration of a quartz mercury lamp. The decrease in radiation appears to be non-selective, or nearly so, for the visible portion and near ultra-violet as compared with the middle and far ultra-violet stopped by 4·0 mm. of Pyrex glass. The Pyrex transmitted 40 per cent, clear Corex A (8·2 mm.) 70 per cent and red-purple Corex A (10·2 mm.) 19 per cent.

Radiation from a mercury arc produces erythema of the skin of the upper arm when it suffices to decompose roughly 0·056 mg. of crystalline oxalic acid per sq. cm. in 3 minutes, under standard conditions.

Changes in a mercury arc may be followed with a glass vacuum sodium photo-electric cell of the Burt type. The 4 mm. Pyrex sheet transmitted enough radiation to produce a current 75 per cent of that with unscreened cell; the red-purple Corex A transmitted 33 per cent with a new lamp and 30 per cent with a lamp which had been in use for 360 hours. Double surface-flashed opal glass, 1·8 mm. thick, cut down the current to 46–47 per cent. Owing to the fact that the cell is not equally sensitive to radiation of different wave-lengths these figures are not percentages of the energy transmitted.

When first switched on the radiation from a mercury arc on a 200-volt town supply (A.C.) falls to about one-half of its initial value within a little over a minute. It then increases rapidly, reaching a maximum approximately fifteen times the minimum value within 5 or 6 minutes from the start.

W. R. G. A.

Methods for the Photo-electric and Photo-chemical Measurement of Daylight.

By W. R. G. Atkins and H. H. Poole.

Report of the Conference of Empire Meteorologists, Agricultural Section, London, 1929, *pp.* 67–89. *Reprinted in Biological Reviews,* 1930, **5**, 91.

The photo-electric current may be measured by suitable (portable) galvanometers, or continuously by means of a recording galvanometer. The potentiometer null method (H. H. Poole) can be used at sea, as can also the neon lamp method (J. H. J. Poole) which integrates the current over a short period and thus gives a measure which is independent of the large variations from moment to moment, caused by waves. Integration over longer periods may be carried out at sea or on shore by photo-electric production of alkali or deposition of copper.

The colour sensitivity, standardisation and constancy of photo-electric cells are discussed, also the optical conditions to be considered in such measurements.

The authors' previous photo-electric work is summarised, especially with regard to seasonal changes in illumination.

W. R. G. A.

The Action of Adrenaline and of Certain Drugs upon the Isolated Crustacean Heart.

By W. A. Bain.

Quart. Journ. Exp. Phys., Vol. XIX, 1929, *pp.* 297–308.

The effect of Adrenaline, Ephedrine, Ergotoxine, Pilocarpine, and Atropine upon the isolated perfused heart of the crabs *Maia squinado*, *Cancer pagurus*, and *Carcinus mœnas*, is described and eleven tracings given. The perfusion method adopted is described, the perfusion medium being sea-water adjusted to a suitable pH by means of hydrochloric acid —all fluids used in any one experiment having the same pH.

Adrenaline, in all active concentrations, is accelerator and, in the case of Cancer, augmentor in addition. Ephedrine, on the other hand, has no action on the crab heart. Ergotoxine is depressant, but it neither antagonises nor reverses the adrenaline effect. Pilocarpine (1/10,000) produces an action similar both qualitatively and quantitatively to that obtained with adrenaline (1/40,000), but the effect is immediately abolished by atropine sulphate (1/250,000) whereas the adrenaline effect cannot be so abolished even with the concentration of atropine as high as 1/40,000.

The almost identical nature of the response obtained with adrenaline and pilocarpine respectively suggests that a similar mechanism is responsible for each. The failure of atropine to abolish the action of adrenaline shows that this can hardly be so ; further, the similar failure of ergotoxine demonstrates that the conditions obtaining in the crustacean heart with respect to adrenaline may not be strictly comparable with those obtaining in the vertebrates.

W. A. B.

Influence of Age on the Temperature Coefficient of the Respiration Rate in Leaves of *Scolopendrium scolopendrium* Karst.

By J. Bělehrádek and M. Bělehrádková.

New Phytologist, Vol. XXVIII, 1929, *pp.* 313–318.

Oxygen intake in leaves of *Scolopendrium scolopendrium* Karst. under varied temperature was measured and it was found that the temperature cœfficient first increases and then decreases with the age of the leaves. Variations of temperature cœfficient with age, found in these experiments, are analogous to those previously described in animals. They are explained by the hypothesis that colloidal changes occur in the protoplasm with age, and that these are accompanied by variations of the viscosity, and thus of the rate of diffusion, in the reacting protoplasmic phases.

J. B.

On the Feeding Mechanism of the Copepods, *Calanus finmarchicus* and *Diaptomus gracilis*.

By H. Graham Cannon.

Brit. Journ. Exper. Biol., Vol. VI, No. 2, 1928, *pp.* 131–144.

Calanus finmarchicus and *Diaptomus gracilis* both feed automatically when swimming slowly and steadily through the water. A feeding current is produced which is filtered by the stationary maxillæ. Food so obtained is passed on to the mandibles by the maxillulary endites and setæ on the bases of the maxillipeds. The feeding current is a vortex passing through the mouth parts which results automatically from the swimming activities of the antennæ, mandibular palps and maxillules. The feeding vortex is caused to pass through the maxillæ by the combined activities of the maxillipeds and the maxillulary exites. The former suck water into the filter chamber between the maxillæ while the latter suck it out through the maxillary setæ. The views of Storch and Pfisterer on the feeding mechanism of *Diaptomus gracilis* are criticised. There is no

powerful antero-posterior swimming current as described by these authors. The swimming current is in the form of a vortex encircling the body and most marked at the sides in the angle between the body and the antennules. H. G. C.

The Histology of the Alimentary Tract of the Plaice (*Pleuronectes platessa*).

By Ben Dawes.

Q.J.M.S., Vol. 73, *Part II, Oct.* 1929, *pp.* 243–274.

The alimentary tract of the plaice consists of the following regions: pharynx, œsophagus, stomach, duodenum intestine and rectum. In the pharyngeal and œsophageal regions the mucosa of the tract is intensely folded and the epithelium is liberally beset with goblet cells. Taste-buds occur in the pharynx, which is devoid of glands as is also the œsophagus. The œsophagus is sharply defined from the stomach. Gastric glands occur in all parts of the gastric mucosa, being shallower at the cardiac end of the organ. Each gland consists of 3 types of cells, columnar cells lining the crypt, cubical, mucus-producing cells forming the neck of the gland tubule, and granular cells forming the base of the tubule. Parietal or oxyntic cells do not occur, nor do goblet cells, in any part of the gastric epithelium. The intestinal mucosa is folded so as to simulate crypts and villi, but these structures do not occur. There is no differentiation of the epithelium except into goblet cells. Leucocytes probably do not play any important part in food absorption. The pyloric cæca exhibit the same histological structure as the intestine and probably perform similar functions. A well-developed valve occurs at the junction of the intestine and the rectum. B. D.

The Early Prophases of the First Oocyte Division as seen in Life in *Obelia geniculata*.

By G. H. Faulkner, B.Sc.

Q.J.M.S., Vol. 73, 1929, *pp.* 225–242.

The nucleolus of the resting oocyte contains the whole of the chromatin of the nucleus. During the early growth phases the nucleolus elongates and then divides by a series of transverse fissions into fragments, each of which is a condensed pair of chromosomes. The two members of each pair subsequently separate and finally break down into a group of globules and are thus dispersed. The two members of the largest bivalent chromosomal element are unequal and probably represent an XY pair. The whole account is based on observations made on the living oocyte.

G. H. F.

Lipin Secretion in Elasmobranch Interrenal.

By A. H. H. Fraser, M.B., Ch.B., B.Sc.

Q.J.M.S., Vol. 83, 1929, *pp.* 121–134.

The paper describes the results of an intensive histological study of the interrenal of about thirty rays (*Raya clavata*). It was found that while the majority of glands correspond to the usual description of an ochre-yellow body, with the lipins confined to its constituent cells, a minority (about one in ten) show a brown coloration of varying intensity. When sectioned, these brown glands show evidence of active lipin secretion, in some cases the greatest concentration of lipin being in the interlobular capillaries.

Further, it is shown that in addition to the ordinary lobule commonly figured, the interrenal may show hypertrophied lobules, disintegrating lobules, and acini.

These various and histological pictures are interpreted as phases in a definite cycle of glandular activity, viz. :—

1. Resting lobule.
2. Distension of lobule.
3. Disintegration of lobule.
4. Formation of acinus.
5. Collapse of acinus.
6. Reformation of resting lobule.

From the acini a massive secretion of lipin takes place into the interlobular capillaries. The physiological importance of this phenomenon is emphasised.

The occurrence of melanin pigment in a minority of the glands is described, and evidence submitted of a relationship between the formation of melanin and the secretion of lipin. A. H. H. F.

Methods of Estimating Phosphates and Nitrates in Sea-Water.

By H. W. Harvey.

Cons. Perm. Internat. Rapp. et Proc. Verb. LIII, 1929, *pp.* 68–74.

Existing methods of estimating phosphates and nitrates in sea-water are reviewed and possible sources of error discussed. A colourimeter is described for more exact estimation of the very faint blue produced in the Atkins-Denigès method with sea-water containing less than 15 milligrams P_2O_5 per cubic metre, also a colourimeter for the rapid estimation of phosphate in sea-water samples on board ship. The former was demonstrated at the Conference held in October, 1928, at Oslo, where a more

robust instrument embodying the same principles was designed and later made by Messrs. Hellige to the order of Professor Johan Hjort. (See also "Report on the results of special investigations conducted at the University of Oslo in October, 1928," by Buch, Gaarder, Grau, Harvey, Schreiber, and Wattenberg, *ibid.*, pp. 95–115.)

H. W. H.

Hydrodynamics of the Waters South-East of Ireland.

By H. W. Harvey.

Journ. du Conseil, Vol. IV, 1929, *pp.* 80–92.

A simple method is described of calculating the velocity and direction of ocean currents from the distribution of density in the sea. The theoretical grounds on which this method, and a similar calculation by Werenskiold, rest are given. A comparison of the results obtained by this simple and rapid method, with results obtained by applying Bjerknes' Theorem, shows that the differences are not likely to exceed 5 per cent, which is of little consequence.

The currents, set up by differences in density, in the upper 60 metres of the sea lying to the south-east of Ireland, form a current system which is similar to the movement of the whole body of water as deduced by Matthews from the distribution of salinity.

The application of Bjerknes' Circulation Theory to this area, subject only to extremely slow currents, yields results which conform with conclusions based on entirely different evidence.

H. W. H.

The Maintenance of Life and Irritability in Isolated Animal Tissues.

By A. V. Hill, F.R.S.

Nature, Vol. 123, 1929, *pp.* 723–730.

This paper represents the Ludwig Mond Lecture delivered at the University of Manchester on March 6th, 1929. It refers to the conditions under which survival of isolated animal tissues can be secured, particularly in reference to their study in the laboratory. The influence of oxygen in maintaining the normal state is discussed. Reference is made to the experiments of Levin and of Furusawa on the "depolarisation" of crustacean nerve, and on the utilisation of oxygen by this nerve in maintaining its state or readiness to respond to a stimulus.

A. V. H.

The Heat Production and Recovery of Crustacean Nerve.

By A. V. Hill, F.R.S.

Proc. Roy. Soc. B., Vol. 105, 1929, *pp.* 153–176.

Levin, in 1927, published an account of certain new observations upon the electric change in stimulated crustacean nerve, and these observations were confirmed and extended by Furusawa in a paper published in 1929. It appears from these investigations that these non-medullated nerves are in a sense "depolarised" by activity and that in the presence of oxygen a recovery process occurs in which the state of polarisation is restored. The electric signs of activity in such nerve are much larger than in ordinary medullated nerve, and it seemed likely that an examination of the heat production during recovery might throw considerable light upon the process of restoration after activity.

The total heat per second of maximal stimulation is many times greater than in frog's nerve, and there is a clear division into two phases, initial and recovery. The initial process, completed during stimulation, yields only about two and a quarter per cent of the total heat. The recovery process, lasting for about 25 minutes at 16° C., supplies the remainder. The ratio of recovery to initial heat is about five times as great as in the case of frog's nerve. The result shows the importance of oxidative recovery, and confirms Furusawa's hypothesis that in the presence of oxygen a crab's nerve, "depolarised" by activity, is recharged by an active combustion process.

The limb nerves of Maia form an admirable preparation for such research.

A. V. H.

The Precipitation of Calcium and Magnesium from Sea-Water by Sodium Hydroxide.

By Eleanor M. Kapp.

Biological Bulletin, Vol. LV, No. 6, 1928, *pp.* 453–458.

Sea-water, after the addition of varying amounts of NaOH, was analysed for the amount of Ca and Mg left in solution. It was found that the amount of these ions precipitated depended on (1) the amount of NaOH added; (2) the concentration of carbonate in the sea-water; and (3) the extent to which equilibrium had been attained in the mixture.

E. M. K.

Lankester's "Gregarine" from the Eggs of *Thalassema neptuni*.

By D. L. Mackinnon and H. N. Roy.

Nature, Dec. 7, 1929.

Among twelve female specimens of *Thalassema neptuni* Gärtner examined at Plymouth, eight showed the developing eggs (in the nephridial sacs) heavily infected by a sporozoan. This is apparently the parasite described by Lankester (1881) as a "gregarine." Our preliminary investigation shows, however, that it is a coccidan. The adult trophozoite is a worm-like organism, which may reach the length of 400μ. We have noted all the main stages in development of the gametes and sporoblasts, and are continuing our investigation in the hope of demonstrating the schizogonic portion of the life-cycle and of determining the systematic position more exactly.

D. L. M. AND H. N. R.

Regeneration and Fragmentation in the Syllidian Polychætes (Studies on the Syllidæ. II).

By Yô K. Okada.

Arch. f. Entwick-mech. Bd. CXV, 1929, *pp.* 542–600.

Syllids regenerate easily the posterior segments, if the extremely anterior part is not cut, but anterior regeneration is variable according to the species employed. The regeneration capacity in *Syllis gracilis* and *Procerastea Halleziana* is limitless, and there is a complete recovery of the missing part, including a new formation of the entire system of the pharyngeal apparatus. In *Autolytus pictus* the anterior (before the 13th set. segment), the middle (from the 14th to 42nd set. segment) and the posterior part of the body behave quite differently in respect to their faculties of regeneration.

Fragmentation can be artificially caused by changing the salinity of the sea-water in which the experimental worms are kept (by adding fresh water according to E. J. Allen, 1921), or by subjecting the worms to a solution of KCl. In the first case a change of the osmotic pressure in the intestinal cavity would seem to be the main cause of the process of breaking, while in the latter case the fragmentation would seem to be provoked by an unusually strong constriction of the longitudinal muscles of the segments. The position of breaking is, however, predetermined by the special arrangement of megasepta, the presence of which can be seen by external observation through the transparent integument, as a particularly deep constriction in the alimentary tract.

Yô K. O.

On the Physiology of Amœboid Movement. V. Anærobic Movement.

By C. F. A. Pantin, M.A.

Proc. Roy. Soc. B., Vol. 105, 1930, *p.* 538.

The effect of lack of oxygen on a marine "Limax" amœba has been studied. Several methods have been used to remove oxygen.

In the absence of oxygen, gradually diminishing amœboid movement continues for 6 to 12 hours. The amœba then abruptly passes into an inactive condition. Anærobic activity is accompanied by morphological changes and an apparent rise in protoplasmic viscosity. There is a definite relation between the velocity of movement and the duration of anærobiosis.

Movement continues not only when oxygen is completely absent, but when the external medium has considerable reducing power.

Evidence is given that the energy of amœboid movement is supplied by an anærobic process, which allows movement to continue in the absence of oxygen.

It is suggested that the progressive diminution of anærobic movement is related either to the exhaustion of a precursor of the anærobic process or, more probably, to the accumulation of products of this process.

Oxygen is required for recovery after anærobiosis; this recovery occurs even after 48 hours, but anærobic inhibition of movement is ultimately irreversible. It is concluded that the anærobic processes of amœboid movement are normally accompanied by an oxidative recovery process.

Recovery is progressively delayed as the period of anærobiosis is increased beyond about 6 hours. Delayed recovery occurs in two stages; the amœba is at first inactive, and then suddenly resumes activity, as in immediate recovery. The delay is caused by increase in duration of the inactive phase. Delay in recovery increases long after all activity in the anærobic amœba has ceased, and is therefore not altogether dependent on activity. The delay may be related to the accumulation of an "oxygen debt."

The analogy with muscular and other forms of contractile activity is discussed.

C. F. A. P.

On the Physiology of Amœboid Movement. VI. The Action of Oxygen.

By C. F. A. Pantin, M.A.

Proc. Roy. Soc. B., Vol. 105, 1930, *p.* 555.

The effect of different partial pressures of oxygen on the movement of a marine amœba has been investigated.

With a limited oxygen supply, movement diminishes and ceases. But its duration is greatly prolonged when a trace of oxygen is present as compared with the duration under complete anærobiosis. The duration of movement increases with the oxygen pressure. After complete anærobiosis oxygen is required for recovery; prolonged activity in the presence of a trace of oxygen may therefore be due to this recovery process operating to a limited extent.

After a given duration of oxygen deficiency, the greater the deficiency has been the greater is the time required for the amœba to recover in aerated sea-water. The efficiency of the recovery process during oxygen deficiency therefore diminishes with the oxygen pressure.

As an oxygen pressure of 30–40 mm. Hg is approached the activity of the amœbæ increases. Above this critical pressure movement is maintained as long as in controls in aerated sea-water. Reduction of activity below this critical pressure does not seem to be related to difficulty of diffusion of oxygen into the amœba but to the diminished efficiency of the recovery process itself in the presence of insufficient oxygen.

The relation of the critical pressure to the oxygen pressure of the environment is discussed.

C. F. A. P.

On the Physiology of Amœboid Movement. VII. The Action of Anæsthetics.

By C. F. A. Pantin, M.A.

Proc. Roy. Soc. B., Vol. 105, 1930, *p.* 565.

The effect of certain anæsthetics on a marine amœba has been studied. The morphological changes and other effects of cyanide (below 10^{-1}M.) resemble those of oxygen deficiency. Activity progressively falls to zero; "Limax" movement is maintained till inhibition occurs. Inhibition is reversible even after 40 hours in 10^{-1}M. cyanide.

The effects of cyanide on the amœbæ are characteristic of its action on a respiratory mechanism. The minimal effective concentration lies between

10^{-5} and 10^{-6}M. Increasing the concentration to 10^{-1}M. only slowly increases the effect. The effect of a given cyanide concentration can be matched with that of a given oxygen deficiency in the medium.

The effects of cyanide recorded differ from the cytolytic effects recorded by Hyman in fresh-water amœbæ. It is suggested that such cytolysis is not due to cyanide, but to the great alkalinity and unbalanced potassium-ion concentration of KCN solutions.

The effects of sulphides on the marine amœba closely remembles that of cyanides.

Alcohols and chloretone cause inco-ordination of amœboid movement. At a certain liminal concentration movement becomes irregular, and it is inhibited by about 10 times this concentration. The effects do not resemble oxygen deficiency. The effectiveness follows the series methyl< ethyl < butyl and chloretone < amyl.

In the absence of oxygen, cyanides do not effect the behaviour of the amœbæ. This agrees with the supposition that cyanides act upon the respiratory mechanism in the amœba. Alcohols are even more effective in the absence of oxygen than in its presence.

Those anæsthetics (cyanides and sulphides) which induce effects resembling oxygen deficiency in the amœba are those which inhibit the cytochrome respiratory mechanism. It is suggested that the adverse effects produced by the anærobic processes causing amœboid movement are normally removed by an oxidative recovery process, which involves some respiratory mechanism similar to cytochrome.

C. F. A. P.

The Gregarines of Cucumaria; *Lithocystis minchinii* Woodc. and *Lithocystis cucumariæ* n.sp.

By H. Pixell-Goodrich, M.A., D.Sc.

Q.J.M.S., Vol. 73, 1929, *pp.* 275–287.

Cucumaria saxicola Brady and Robertson is shown to contain two neogamous gregarines whose life-histories have hitherto been confused with one another. One of these, *Lithocystis cucumariæ* n.sp., is exceptional in passing through all its stages in the respiratory trees of its host where the cysts form conspicuous opaque white spheres, up to ·5 mm. in diameter, easily seen on opening the body cavity. There is little doubt that spores enter and leave the host with currents of water through the cloacal aperture. This parasite has spores with long flattened tails similar to the type species, *L. schneideri* Giard, from Spatangoids.

About 18·5 per cent *C. saxicola* from Wembury Bay, Mewstone and Stoke Point were found to be infected.

The other gregarine, *L. minchinii* Woodc., is enclosed throughout most of its life in a cup-like outgrowth of the host's cœlomic epithelium and connective tissues. Its spores have peculiar episporal processes including a short tail.

From the same regions mentioned above, 40 per cent of the *C. saxicola* were infected with this species.

H. P. G.

The Comparative Morphology of the Elysioid and Æolidioid Types of the Molluscan Nervous System, and its Bearing on the Relationships of the Ascoglossan Nudibranchs.

By Lilian Russell, M.Sc.

Proc. Zool. Soc., London. Part 2, 1929, *pp.* 197–233.

Since Souleyet posed the problem of the phylogenesis of the Elysioid type in 1852, the taxonomists have solved it in one of two ways. Those impressed by the Æolidioid external morphology of Hermæa and Stiliger have included them in the Nudibranchs, while the close resemblance of the alimentary canal, and especially of the pharyngeal mechanism, in Elysioids and Lophocercoids, has led others to group these two types together as Ascoglossa. The above paper reopens the controversy, using as a criterion that system which has served most consistently as an index of relationship in the Gastropoda. The nervous systems of Elysia and certain Æolidioid types are compared in detail, the territorial distribution of all nerves being determined, and employed in ascertaining the homology of their ganglia of origin. A special attempt is made to render the representation and analysis of the visceral system as complete as possible. By this means the three ganglia of the visceral loop of Elysia are established as true homologues of the three primitive visceral ganglia of the Gastropod. This verification of homology makes it impossible to follow Pelseneer in deriving the Elysioids from Æolidioids with a naked visceral loop. It is further shown that the characteristic gastro-œsophageal ganglia have no homologues in Elysia. The Elysioid nervous system thus resembles the Lophocercoid in general plan, in the structure of the visceral system, and in the possession of retractile superficial eyes, auriculate tentacles with an organ of Hancock, genital nerves derived from the abdominal ganglion, and pedally innervated lateral appendages : the author accordingly proposes to sever the unnatural union of the Elysioids with the Nudibranchs, and to place them with their natural relatives, the Lophocercoids.

L. R.

The British Sea Anemones.

By T. A. Stephenson, D.Sc.

Vol. I, Ray Society publications, No. 113, *London*, 1928, *pp.* xiv+148.

This volume contains a general account of the morphology, colouration, development, bionomics and classification of the Actiniaria, with special reference to British forms. The account deals most fully with morphology, and is designed, apart from this, to give an introduction, in outline, to the study of Actinians, of such a nature as to render intelligible a more detailed account of them. It is followed by a classified list of the British species, of which 39 are recognised ; and by a classified and a general list of literature. The second volume will contain full descriptions of the species, and further notes on their natural history. The illustrations in Vol. I represent in colour about half the species, the series to be completed in Vol. II ; beyond this they illustrate morphology, histology, etc., and include a dedication page and some tailpieces after the manner of Forbes' *British Echinoderms*.

T. A. S.

A Contribution to Actinian Morphology: the Genera Phellia and Sagartia.

By T. A. Stephenson, D.Sc.

Trans. Roy. Soc. Edinburgh, Vol. LVI, p. 121.

The most serious gap in our knowledge of the anatomy of the British Actiniaria has been the almost complete absence of structural data referring to the genus Phellia. This paper describes the anatomy of the British forms which have been assigned to the genus ; shows that the genus is heterogeneous ; establishes *P. gausapata* Gosse as the type ; creates a new genus *Cataphellia* for *P. brodricii* Gosse ; and shows that *P. murocincta* Gosse is a form of *Sagartia troglodytes*, whilst *P. picta* Gosse is undoubtedly the young of *S. lacerata*. The status of the genus is discussed, after which the paper goes on to consider other matters. An account of the complex patterns developed on the peristome and tentacles of many anemones is given, and the value of the structure of such patterns as an index to relationships is pointed out. Lastly, the status of those variable species, *Sagartia elegans* and *S. troglodytes*, is discussed.

T. A. S.

Observations on the Function of Peroxidase Systems and the Chemistry of the Adrenal Cortex. Description of a New Carbohydrate Derivative.

By A. Szent-Györgyi.

Biochem. Journ., *Vol. XXII*, 1928, *pp.* 1387–1409.

Peroxidase plants contain a highly active reducing agent, which can be oxidised and reduced by biological systems, playing this way the rôle of a catalyst between different mechanisms of oxidation. The substance was crystallised, and identified as a hitherto unknown carbohydrate derivative, isomer to glucuronic acid. With regard to the chemical structure "hexuronic acid" is proposed for the name of the substance.

It is shown, that the adrenal cortex of mammals contains a strong reducing agent, specific for this organ. The substance has been isolated and found to be identical with "hexuronic acid" isolated from plants.

It is shown, that the interrenal bodies of elasmobranch fishes (*Scyllium canicula*) contain a strong reducing agent, which is specific for this organ, and shows the same reactions as the hexuronic acid of the mammalian adrenal cortex.

Chemical and physical properties of the hexuronic acid are described (M.P. 175–189, $[\alpha]_D^{21^\circ} = +24^\circ$).

The substance is studied in its relation to different biological oxidation systems. It is shown, that the substance gets oxidised in all systems, in which a phenol is oxidised to a quinone. The substance is not oxidised by the indophenoloxidase of animal tissues or by hæmatine compounds (cytochrom). The hexuronic acid is strongly reduced by the Hopkins glutathion system.

A. S.-G.

A Habit of the Common Periwinkle (*Littorina littorea* Linn.).

By D. P. Wilson.

Nature, *Vol. CXXIV*, 1929, *p.* 443.

On shores where there is little or no growth of the larger Fucoid algæ the periwinkles clinging to the boulders may be exposed to the sun for long periods. The risk of desiccation is lessened by the periwinkle's habit of sticking itself to the rock by secreting a film of mucus between the lip of its shell and the rock surface. This film soon dries, becoming brittle, and the mollusc then retracts and closes the opening of its shell with its operculum. On a steeply sloping surface it is nearly always orientated with the lip of the shell uppermost, the position in which there is least tendency for it to topple over.

D. P. W.

Marine Biological Association of the United Kingdom.

Report of the Council, 1929.

The Council and Officers.

The four usual meetings of Council have been held, at which the average attendance has been sixteen. The thanks of the Council are due to the President and Council of the Royal Society, in whose rooms the meetings have been held.

A Committee of seven members of the Council visited and inspected the Plymouth Laboratory and discussed with the members of the staff the scientific work upon which they were engaged. At the same time a sub-committee of the Fishery Advisory Committee of the Development Commission visited Plymouth and discussed the work of the Laboratory and organisation with the Committee of Council.

We have to record with regret the death of our President, Sir Edwin Ray Lankester, to whose energy, initiative and love for the science of Biology the foundation of the Association in 1884 was chiefly due. He was at first the Hon. Secretary, and as such was responsible for the collection of funds, the organisation of the Association and the building and equipment of the Laboratory at Plymouth. In 1890 he succeeded Professor Huxley as President, an office which he held until his death. To the last he followed with interest the details of the work that was done in the Laboratory, and had the welfare of the Association at heart.

Reference must also be made to the death of Mr. Walter Heape, the first Superintendent of the Laboratory, who was stationed at Plymouth while the erection of the building was in progress.

The Plymouth Laboratory.

The general good condition of the Laboratory buildings has been kept up, the outside painting of the Allen building and of the North building having been carried out. The walls of the ventilating shaft of the tunnel from the main Laboratory to the cliff under the road, which were showing

signs of decay, have been re-pointed, and the Plymouth Corporation have rebuilt the wall facing the road.

A new brick building 20 feet by 18 feet has been erected in the corner of the Citadel wall, behind the Allen block. This is used for the housing of the preserved dog-fish tanks and other specimens, and for the preparation of the dog-fish for preservation; it has given a considerable increase of storage accommodation in the old receiving-room in the main building. The latter room has been repaired and redecorated.

The engines and pumps for circulating sea-water through the aquarium and Laboratory tanks have worked efficiently throughout the year and no considerable repairs have been necessary.

The Ship and Motor-Boat.

The steam drifter *Salpa* has run satisfactorily, and has kept workers well supplied with the varying material required for a wide range of research. At the end of October the vessel proceeded to Dartmouth to undergo Lloyd's full-time survey and reconditioning. The work is being done by Messrs. Philip and Son.

The motor-boat *Gammarus* has been used continuously throughout the year for collecting in the Sound. One of the 3-h.p. motors has been replaced by a 6-h.p. Kelvin engine, the old motor being kept as a spare. The new engine has given a satisfactory increase in speed.

The Staff.

Dr. J. H. Orton, Chief Naturalist at the Laboratory, who first joined the staff in 1910, left at the end of September, on his appointment as Derby Professor of Zoology in the University of Liverpool.

Mr. C. F. A. Pantin, who held the post of Physiologist, left at the same time, on election to a Fellowship at Trinity College, Cambridge, and to a Lectureship in the same college.

Mr. V. C. Wynne-Edwards, one of the two student-probationers, left in August, having been appointed Lecturer in the Zoological Department of Bristol University.

Mr. F. S. Russell, who returned from the Great Barrier Reef Expedition in March, has been promoted from Assistant Naturalist to Naturalist, and has also undertaken the duties of Administrative Assistant, previously carried out by Mr. H. W. Harvey.

The post of Physiologist is being filled by the appointment of Dr. C. M. Yonge, the leader of the Great Barrier Reef Expedition, who was previously an Assistant Naturalist at Plymouth. Dr. Yonge will take up the appointment in January (1930) on his return to this country.

Mr. G. A. Steven, Student-Probationer, was promoted to Assistant Naturalist in October, in place of Mr. F. S. Russell.

Mr. G. M. Spooner of Christ's College, Cambridge, and Mr. J. S. Colman of New College, Oxford, who has been a member of the Great Barrier Reef Expedition, have been appointed Student-Probationers.

Another member of the Great Barrier Reef Expedition, Mr. A. G. Nicholls of Perth, Western Australia, has been sent to the Laboratory for a year by the Australian Commonwealth Council of Scientific and Industrial Research as a research worker.

Dr. Atkins gave a course of lectures on the methods for the photo-electric and photo-chemical measurement of light at the Imperial College of Science for the University of London, and also read a paper on the same subject, and demonstrated the apparatus used in his investigations to the Conference of Empire Meteorologists.

Mr. Pantin gave a course of lectures, with practical work, on General Physiology, at University College, London, and at Cambridge during the spring term.

Meetings at the Laboratory.

As already mentioned, a sub-committee of the Fisheries Advisory Committee of the Development Commission visited the Laboratory in March. The sub-committee consisted of Sir William Hardy, F.R.S. (Chairman), Sir John Marsden, Bart., Prof. G. Barger, F.R.S., Prof. G. I. Taylor, F.R.S., Dr. E. S. Russell, and Mr. E. H. E. Havelock (Secretary).

In April the International Council for the Exploration of the Sea, which was meeting in London under the Presidency of Mr. H. G. Maurice, C.B., came to Plymouth to see the Laboratory. The members of the staff and naturalists working at the Laboratory prepared exhibits illustrating their researches, which they demonstrated to the members of the Council on the afternoon of April 16th, and on the evening of that day the Council was entertained to dinner by the Mayor of Plymouth. On the following morning a joint meeting of the International Council and of the "Challenger" Society, which was attended by representatives from the other British Marine Laboratories, was held in the room used for our Easter classes. At this meeting scientific papers were read and useful and stimulating discussions took place.

In June the Physiological Society held a meeting at the Laboratory, when the work of the staff was again demonstrated, and the staff and visiting workers took part in the meeting of the Society.

The Council recognise that meetings of this character have a most stimulating effect on the scientific activity of the Laboratory.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year :—

Dr. C. Amirthalingam, London (Bionomics of oysters. Effect of temperature on fertilisation of Pecten).
Miss D. Atkins, London (Pinnotheres and Loxosoma).
C. Baschlin, Basle (Hydroids. Cytology).
R. Bassindale, Sheffield (Morphology of *Balanus balanoides*).
L. C. Beadle, Cambridge (Regeneration in Hydroids).
Dr. J. J. Bek, Utrecht (pH Estimations. Carnivorous Crustaceans and Prosobranchs).
A. L. Bennett, Cambridge (Sexual characters of Fishes).
N. J. Berrill, Montreal (Regeneration of Polychætes. Development of Ascidians).
Miss A. Bidder, Cambridge (Digestion in Loligo).
Dr. Cecil von Bonde, S. Africa (Fisheries).
Dr. H. Blaschko, London and Berlin (Excitation of Maia nerve).
Miss M. A. Borden, Canada and London (Respiration of marine invertebrates).
Miss E. M. Brown, London (Chemistry of sea-water).
Dr. G. P. Chandler, London (Action of nitrites on muscle).
Mademoiselle Choucroun, Paris (Mitogenetic rays).
G. L. Clarke, Harvard (Phototropisms of planktonic crustacea).
Miss M. H. Collet-Brown, Plymouth (Diatoms).
Miss C. I. Dickinson, Kew (Marine Algæ).
J. R. Dymond, Toronto (General Zoology).
Dr. N. B. Eales, Reading (General Zoology).
Miss G. H. Faulkner, London (Budding in Alcyonidium).
Dr. H. Fawzy, Egypt (Spermatogenesis and oogenesis in the Soles).
Prof. H. M. Fox, Birmingham (Spectrographic analysis of animal tissues).
Miss L. Garnjobst, Stanford, U.S.A. (Encystment in Protozoa).
Prof. E. S. Goodrich, F.R.S., Oxford (Annelids).
Dr. Pixell-Goodrich, Oxford (Parasitic Protozoa).
P. A. Gorer, London (Crustacean inhibitory nerves).
A. Graham, Edinburgh (Digestion in Anemones).
Dr. A. J. Grove, Sheffield (Biology of *Melinna adriatica*).
Dr. R. Gurney, Oxford (Larval Copepods).
T. J. Hart, Leeds (Life-history of Corophium).
E. Heron-Allen, F.R.S., London (Foraminifera).
Prof. A. V. Hill, F.R.S., London (Heat production of crustacean nerves).
A. D. Hobson, Edinburgh (General physiology of eggs. Echinus, etc.).
Dr. E. G. Holmes, Cambridge (Metabolism of crustacean nerve).
Prof. Sir F. G. Hopkins, Cambridge (Glutathione).
Dr. S. L. Hora, Calcutta (General Zoology).
A. Howard, Mawson Expedition (Hydrography).
Dr. J. J. Izquierdo, Mexico (Cardiac sympathetic phenomena).
Dr. I. Kahn, Moscow (Nerves of Maia).
P. Kirtisinghe, Ceylon and London (Enteric plexus in Fish).
D. J. Malan, Pretoria (Planarians and Cyanides).
Dr. K. Mansour, Egypt (General Zoology).
Miss I. Manton, Manchester (Algæ).
C. Matheson, Cardiff (Hydrography).
A. A. Nayal, Egypt (Marine Algæ).

Miss G. L. Naylor, Plymouth (Distribution of marine lichens and chemistry of cell wall of Fucoids).
A. G. Nicholls, Perth, Australia (General Zoology).
Miss E. A. T. Nicol, Edinburgh (Physiology of digestion in Sabella).
E. Ogden, London (Urea in Dogfish and Rays).
Dr. Yô Okada, Kyoto (Schizogamy of the Syllidæ).
R. J. Pumphrey, Cambridge (Action of ions on Mytilus muscle).
Dr. H. S. Rao, Calcutta (Sponges).
H. N. Roy, Calcutta and London (Protozoa of Polychæte worms).
Dr. W. A. H. Rushton, Cambridge (Neuro-muscular mechanism of Maia).
Miss G. F. Selwood, Portsmouth (Oysters).
Dr. K. Sembrat, Lwów, Poland (Cytology).
P. Sen, Calcutta (Plankton and Insects).
Miss F. A. Stanbury, Birmingham (Culture of Diatoms).
F. G. Stott, Manchester (Digestion in *Echinus esculentus*).
Dr. M. A. Thynne, Plymouth (Nematoda).
Dr. F. M. Turner, London (Freshwater Algæ).
Prof. D. M. S. Watson, F.R.S., London (Gas content and mechanism of swim bladder of fishes).
Miss E. J. Weil, Vienna and London (Influence of salt and fresh water on animals).
G. P. Wells, London (General Physiology).
Miss M. A. Westbrook, London (Algæ).
Prof. K. B. Williamson, Malay States (Water analysis).

The usual Easter Vacation Course in Marine Zoology was conducted by Dr. J. H. Orton, and was attended by forty-two students from Oxford, Cambridge, London, Belfast, Manchester, Birmingham, and Reading.

Another Course was held during the Summer Vacation and attended by twenty-two students.

An Advanced Course in Comparative Physiology and Experimental Biology, conducted by Mr. C. F. A. Pantin, was also held during the Summer Vacation and attended by fourteen students.

During the Easter Vacation Dr. E. W. Shann brought a class of four boys from Rugby, Mr. J. M. Branfoot a class of nine from Oundle, two boys from Harrow and one from Malvern, and Mr. H. C. W. Wilson a class of six from Monkton Combe School, Bath.

During Whitsuntide Mr. W. H. Leigh-Sharpe brought a class of eight students from Chelsea Polytechnic.

General Work at the Plymouth Laboratory.

Mr. Ford has devoted another year to the study of the herring and its fishery at Plymouth, and has published a further three papers of the series commenced last year. With the conclusion of observations on the progress of the drift-net fishery in the winter of 1927–28, a survey of the results obtained since the beginning of work in 1924–25 was made, in an endeavour to apply them to the question of the prediction of future

fisheries. This analysis was published in the Journal of the Association, Vol. XVI, of May, 1929. The data collected during the season 1928–29, now under investigation, will be of especial interest with regard to this matter of forecasting.

Young herrings collected from the rivers Tamar and Lynher have been used to gain knowledge of the processes of transition from the transparent larval herring to the fully-scaled and silvery adolescent. A report is nearing completion in which it is shown that the alteration in position of fins and anus, and the changing body proportions during metamorphosis can largely be explained as the consequence of differential growth of the larva. Simple models constructed of tape and elastic have proved very helpful in this study.

During the winter of 1927–28, experiments in artificial fertilisation and hatching of herring eggs under known conditions of salinity were carried out. It was found that eggs could be fertilised and incubated successfully in water varying in salinity from 37·8 to 4·8‰, and that the specific gravity of the larvæ from these eggs was dependent upon the salinity of the water in which the eggs were hatched.

In October last, Mr. Ford and Mr. Steven took the opportunity to visit Grimsby and Billingsgate on their return from a meeting of the "Challenger" Society at Aberdeen. At Grimsby they were fortunate in witnessing the landing of a large catch from Greenland, and in addition were able to learn something of the chemical and bacteriological problems connected with the manufacture of fish-glue.

At Billingsgate they were conducted round the market by the Chief Inspector of the Fishmongers' Company, to whom they are greatly indebted, as well as to Mr. C. N. Hooper, the Clerk to the Company, who made the arrangements.

Dr. Orton has again given as much time as possible to the preparation for publication of his earlier and interrupted researches, while at the same time continuing his studies in Marine Bionomics. Observations on Echinus and Patella extending over a number of years have been summarised and published in the Journal. Some preliminary experiments on the habits of the whelk-tingle *Ocinebra erinacea*, obtained from different habitats, have shown that even young individuals originating from oyster-beds will readily prey upon oysters, whereas larger and (with little doubt) older Ocinebra derived from a situation where oysters seldom occur only rarely attack oysters. This tingle is generally acknowledged by expert conchologists as a widely distributed form and is apparently a good species, according to the accepted criterion of a species. The observations recorded, therefore, show that within an apparently good species considerable bionomical variation occurs involving physiological characters. Similar facts have been elicited in studies on Echinus (migration

and breeding), Patella (shell-shape, shell-structure), and Ostrea (shell-shape, shell-structure, and reproductive rhythm). It is suggested by Dr. Orton that in this kind of variation lies some of the raw material for the process—and the detection of the trend—of Evolution.

An account of experiments in the sea on anti-fouling paints, extending over a period of $3\frac{1}{2}$ years, has been prepared by Dr. Orton for publication in the current number of the Journal. In these researches the growth-inhibitive and preservative values of poisonous paints and other substances (15 substances in all) have been studied side by side with general researches on the rate of growth of Invertebrates. Some chemical analyses of the more important anti-fouling paints investigated were made by the Government Chemist at critical stages of the experiments and are included in the published work. It was found that the fundamental factors determining the capacity of a paint to prevent growth include :

(*a*) great resistance to erosion,
(*b*) a toxicity depending upon slow but efficient ionisation of toxic substances,
(*c*) great capacity to adhere to the surface painted, involving a degree of roughness and dryness of the surface painted.

It was proved by critical chemical analyses that gradual loss of toxicity of the more efficient poisonous paints—after about $2\frac{1}{2}$ to $3\frac{1}{2}$ years' immersion in the sea—was accompanied by gradual diminution of the toxic elements, arsenic, copper and zinc, in the paints. The concentration of toxic elements present in a paint when toxicity is at vanishing point can be determined in the sea biologically, and in this way may be determined the minimum rate of –and data useful for the regulation of —ionisation necessary to ensure toxicity in a given paint. It is believed that many useful practical and interesting biological points arise out of these researches.

The investigation on the variation in shell-shape in Patella in relation to environmental conditions has been continued. In this work a high-shelled form has been found on mussels and stones on Gas Works Island in Teignmouth Estuary, in what is regarded as an abnormal situation, i.e. near low-water neaps. It has been discovered, however, that seed mussels are relaid on this bed from time to time from a high-water situation in the locality. Thus it is possible that shell-form on Gas Works Island is a product of two environments during unknown periods. It is hoped to obtain critical information on the phenomenon by investigating conditions in estuaries in other parts of England where Patella and mussels occur naturally.

It was hoped to publish an account of observations and experiments

on the rate of growth and breeding phenomena in some common Ascidians in the current number of the Journal. The final preparation of the work had to be postponed in September, but it is Dr. Orton's intention to complete this and some other outstanding papers for publication in the future.

The continuous records of hydrographic data between Plymouth and Ushant have been maintained, and continue to be published in the Rapport Atlantique of the International Council. The year 1929 has been of interest, since in June high-salinity water appeared off Ushant and lay to the westward of the mouth of the English Channel. In the Eddystone area the surface layers were unusually warm in late summer, while the deeper water was cooler than in most previous years ; at the end of August *Limacina*, common in warmer waters of more southerly latitudes, was abundant, although the low salinity did not indicate any inflow of Atlantic water having penetrated to this area.

Mr. H. W. Harvey has continued work on the oxidation of reduction products of strychnine, from which a method of estimating nitrates and nitrites had been evolved, samples of pure hydrostrychnine and strychnidene having been presented by the late Professor W. H. Perkin, F.R.S. Meanwhile the firm of Riedel-de Haen of Hannover have placed on the market a solution of reduced strychnine in sulphuric acid, which is satisfactory for this estimation, and probably obviates the need for further investigation at the present juncture. Delegates to the conference concerning methods of estimating nutrient salts in sea-water, held at Oslo in October, 1928, which was attended by Mr. Harvey, have since investigated the distribution of ammonium-nitrogen in the sea, and in connection therewith Mr. Harvey is investigating the direct utilisation of this source of nitrogen by cultures of marine diatoms, and the effect of nutrient salts on their rate of growth.

During the early part of the year Mr. Harvey was engaged in making arrangements for the survey of the River Tees estuary, and has visited the staff at Middlesbrough from time to time.

Dr. Lebour has continued the revision of the account of the Plymouth Marine Fauna, which is nearly finished and includes much new matter, especially as regards the breeding of the various species. It is hoped that it will soon be ready for publication. She has also worked at the crustacean larvæ of the district, giving special attention to those attributed by Sars to *Pandalus borealis* and *Pandalus bonnieri*, which she has now found belong to Caridion. As there were two distinct larvæ and only one known species of Caridion, a second species was searched for and found in the shore-form hitherto understood to be *Caridion gordoni*. It is now established that there are two species of Caridion in the district, one of which is new to science and has been named *Caridion steveni*. To this species

belong the larvæ known as *Pandalus bonnieri*. The adults of the deeper water form, *Caridion gordoni*, have not yet been found near Plymouth (although known from Cornwall), but the larvæ (Sars' *Pandalus borealis*) are common in the plankton and the post-larvæ are occasionally found. The post-larvæ and young of both species have been reared from the respective larvæ in the Laboratory and the young of *Caridion steveni* have been hatched from the egg. A paper on this subject is ready for publication.

Further work on other larvæ is still going on, species of Spirontocaris, Hippolyte, and several other forms having been hatched from the egg. This work on Caridion has cleared up much that was difficult to understand in the relations of the Caridea, and it is hoped that investigations of closely related forms will help still more. Pandalus being of commercial importance in places, it is essential that the larvæ should be rightly identified and easily recognised, and the fact that the two Caridion larvæ have for years been regarded as typical of Pandalus has confused considerably all work on the subject.

The book on Planktonic Diatoms, to be published by the Ray Society, is now in proof form and, it is hoped, will be published early next year.

Mr. F. S. Russell, since his return from the Great Barrier Reef Expedition in March, has been occupied in working up the results of material collected previous to his departure, in continuation of his studies on the vertical distribution of plankton. He has completed a paper on the vertical distribution of young fishes, and this, together with previously published results, gives sufficient data to base general conclusions on what to expect in the behaviour of the commoner species. There is a definite indication of difference in behaviour between the pelagic young of the summer spawners and those of the spring spawners, the former being considerably higher in the water. Routine weekly collections of young fish by oblique hauls with the ring-trawl are being continued, and there is now available information as to abundance of the various species over a period of five years. This will form a useful basis from which to watch for any violent fluctuations that may occur in future years.

Mrs. Sexton's work on the Mendelian inheritance of eye-colour and other factors in *Gammarus*, in which Miss Clark has given valuable assistance, is making progress. Special experiments have been carried out on the effect of breeding and rearing this amphipod at high temperatures, with the consequent production of new mutations. Mrs. Sexton has also been able to do a considerable amount of work in rearing the amphipod *Jassa*, which exhibits marked dimorphism.

Mr. B. Dawes' experiments on the relation between food and growth-rate of Plaice, which are being done at Pier Cellars, Cawsand Bay, for the

Ministry of Agriculture and Fisheries, are showing interesting but somewhat unexpected results. Mr. Dawes has also been able to do a good deal of work on the physiology of digestion of the Plaice.

During the early part of the year Mr. D. P. Wilson completed his researches on the larvæ of the British species of Sabellaria and has published an account of the work in the Journal. He has also continued his efforts to obtain the, as yet, unknown larvæ of a number of common Polychætes, and after many unsuccessful attempts at last succeeded in getting an artificial fertilisation of *Branchiomma vesiculosum*. Only a small proportion of each lot of fertilised ova gave rise to larvæ, which were removed and reared in finger-bowls. These larvæ were of special interest, as little is known about the development of Sabellids. In Branchiomma the pelagic development is short, the larva metamorphosing on the bottom before it is a fortnight old. Specially interesting is the fact that the great branchial crown on the head of the adult arises in the larva as a pair of lobes anterior to the prototroch. Each lobe branches to form a number of filaments and these increase in number as the worm grows older. The young worms have been reared to an advanced stage. The study of the Mitraria larva of *Owenia fusiformis*, commenced last year, has been continued, and this summer further rearings have been made. While living material was available special attention was paid to various obscure points, and especially to the complex system of muscle and nerve strands with which the larva is provided. The relations of these have been worked out as far as possible. A pair of larval nephridia was discovered, but owing to the minute size of the flame cells, and the difficulty of seeing clearly their fine cilia, the structure of these nephridia has not yet been fully made out. The metamorphosis of the Mitraria has been observed on several occasions and previous observations confirmed. A fairly large amount of fixed material, consisting of well-expanded larvæ and young worms, was obtained, and this, after embedding in celloidin and paraffin, is being sectioned for detailed study.

In order to obtain some idea of the bionomic conditions prevailing on the "corner" fishing grounds in the waters off Plymouth, a detailed study of the bottom fauna of the area has been carried out by Mr. G. A. Steven. Quantitative seasonal observations extending over a period of one year (August, 1928-July, 1929, inclusive) have been made, using the 1/10 square metre Bottom Sampler and the "Agassiz" Trawl, a method having been devised for obtaining quantitative hauls with the latter instrument. Investigations into the food actually eaten by the fishes within the area have been carried on simultaneously, over 2000 fishes comprising 29 different species having been examined in the course of the year. The principal food animals present on the "corner" grounds are Annelids and Crustacea. Lamellibranchs, and indeed all

Molluscs, are found only in exceedingly small numbers. Plaice, therefore, which normally depend largely upon molluscan food are very scarce. The only marketable flatfish at all common is the Lemon Sole (*Pleuronectes microcephalus*), which feeds almost entirely on Polychæta and can therefore find sufficient food to support it. When the entire fish population of the area is considered as a whole, it is found that the animals most commonly eaten are those which are most numerous on the ground. Within limits determined by size and by suitability in other respects, the fishes eat the organisms which are at hand. The same species of fish (e.g. Gadoids) trawled off another area on which different bottom animals predominate, reflected this difference in their diet. The feeding habits of a number of fishes have been studied, and close correlation is found to exist between the foraging methods adopted by fishes and the type of food animals normally eaten by them.

River Tees Survey.

Early in the year the Council of the Marine Biological Association undertook to carry out for the Department of Scientific and Industrial Research, a biological and chemical survey of the Estuary of the River Tees, in co-operation with a hydrographical survey undertaken by the Admiralty and a biological and chemical survey of the upper river by the Ministry of Agriculture and Fisheries.

Through the kindness of Sir Charles Parsons, K.B.E., F.R.S., a suitable building in the Cleveland Shipyard, Middlesbrough, was obtained at a nominal rental for use as a laboratory, and a motor-boat was purchased. A scheme embodying the more obvious problems to be investigated was drawn up and approved by a sub-committee of the Water Pollution Research Board, under the chairmanship of Professor G. C. Bourne, F.R.S., and by Dr. H. J. Calvert, the Board's Director of Research.

The Council placed Mr. H. W. Harvey, the Association's Hydrographer, in general charge of the work they had undertaken. Mr. W. B. Alexander, who had had considerable experience of biological research in Australia, was appointed Superintendent of the Laboratory at Middlesbrough, and made responsible for the biological investigation of the estuary. Dr. B. A. Southgate, Mr. W. H. Jackson, and Mr. J. Moor were appointed Physiological Chemist, Chemist and Chemical Assistant respectively. Work at Middlesbrough commenced at the beginning of April. Periodical reports upon its progress are being furnished to the Department of Scientific and Industrial Research, who will be responsible for the publication of the results.

Department of General Physiology.

Dr. Atkins and Dr. H. H. Poole have continued their collaboration on photo-electric photometry and a method was devised for integrating light, by using the photo-electric current to produce alkali or to deposit copper. About one-tenth of a milligram was deposited on a winter day, corresponding to an average vertical illumination of 10,000 metre candles for ten hours. Measurements were also made of the daylight factor in buildings and of the changes in the character and intensity of the light from a mercury vapour arc lamp. The uranyl oxalate method of daylight photometry was also standardized photo-electrically and the photochemical and photo-electric methods were compared in submarine work.

Dr. Poole was unable to visit Plymouth, but Dr. Atkins worked in Dublin for some weeks and a new submarine photometer was made in Trinity College and standardised in the laboratory of the Royal Dublin Society. This photometer has several improvements and is specially suited for the measurement of horizontal illumination. It has been used in conjunction with Dr. J. H. J. Poole's neon lamp photometer. This gives a time-integration and so enables one to measure the light immediately below the surface, where it is very unsteady.

Attention is now being paid to the changes in the colour of daylight under various conditions, using a new type of cell developed by the General Electric Co.

Work on the preservation of fishing nets was limited to the routine testing of nets already in water. Though the copper soap and tar treatment is most effective, it has been found that repeated treatments according to Dr. Olie's (Dutch) method give very good results. The cost of the reagents, cutch, followed by ammoniacal copper sulphate, is low.

Owing to the accumulation of data and the lack of an assistant, work on the minor constituents of sea-water had to be abandoned in the spring. This proved particularly unfortunate as meteorologically the year was a most exceptional one, in which well-marked differences in the normal plankton production might have been expected. The results already obtained are being prepared for publication. Interest centres in the variation in the dates at which the main phosphate consumption takes place in different years, also in the unequal rates of regeneration of phosphate and nitrate. In this connection a study was made of nitrite in sea-water. In the deeper cold water at Station E1 larger quantities of nitrite were found than have ever been recorded for sea-water, but only at the period (August) when nitrate regeneration was actively in progress. The production of nitrite is thus an indication of nitrate production and

can be tested for very readily. The difference between 20 metres on August 16th, 1928, at E1, with 0·2 mg. nitrite nitrogen per cubic metre and 25 metres with 38·3 mg. was most striking, the one showing an almost imperceptible pink with the reagents, the other a deep red.

Mr. Pantin has commenced a series of experiments to determine the action of ions on crustacean muscle. Though much work has already been done on the action of ions on rhythmically contractile organs such as the heart, there is much uncertainty in the interpretation of results on account of the complexity of these organs. By perfusing crustacean skeletal muscle with solutions of known composition and testing the excitability of the muscle with electric stimuli of known intensity, the effects of ions on the contractile mechanism and on the excitation mechanism are readily analysed and separated. A preliminary report of the methods has appeared in the Proceedings of the Physiological Society.

The results cannot yet be fully discussed, but it appears that the mechanisms of excitation and contractility in the cell cannot be treated entirely as separate entities, as has usually been assumed.

Preliminary experiments have also been performed on the effects of ions on the adaptation of *Gunda ulvae* to fresh-water and marine conditions. This organism is commonly subjected to violent changes in the salt content of the external medium. Fräulein E. Weil, working this summer under the direction of Mr. Pantin, found that the organism was able to withstand these changes by allowing the free passage of water in and out of its tissues. Subsequent work by Mr. Pantin indicates that this passage of water is controlled by the cations present in the medium.

The Library.

The pressure on the available space for shelves in the Library, to which attention was drawn in the Report of the Council last year, has become much more pronounced, and it is now a very difficult matter to store the new books, as they are being added from day to day. The erection of a new Library building has become most important ; for the proper storage of books, so that ready access to them is possible, is essential to the efficient working of a Marine Laboratory.

The thanks of the Association are again due to numerous Foreign Government Departments, and to Universities and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the Journal. Thanks are also due to those authors who have sent reprints of their papers, which are much appreciated.

Published Memoirs.

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The Council wish to express their gratitude to the Development Commissioners for their continued support of the work of the Association. They have to thank also for generous grants the Fishmongers' Company (£600), the British Association (£50), the Royal Society (£50), the Physiological Society (£30), the Ray Lankester Trustees (£20), the Universities of Cambridge (£105), Oxford (£52 10s.), London (£52 10s.), Bristol, Birmingham, Leeds, Manchester, Sheffield and the Imperial College of Science.

Officers, Vice-Presidents, and Council.

The following is the list of gentlemen proposed by the Council for election for the year 1930–31 :—

President.

Lieut.-Col. The Right Hon. WALTER E. GUINNESS, D.S.O., M.P.

Vice-Presidents.

The Duke of BEDFORD, K.G.
The Earl of STRADBROKE, K.C.M.G., C.B., C.V.O.
The Earl of IVEAGH, C.B., C.M.G.
Viscount ASTOR.
Lord ST. LEVAN, C.B., C.V.O.
The Right Hon. Sir AUSTEN CHAMBERLAIN, K.G., M.P.
The Right Hon. NOEL BUXTON, M.P.
Sir W. B. HARDY, F.R.S.
GEORGE EVANS, Esq.
Sir NICHOLAS WATERHOUSE, K.B.E.
Prof. W. C. MCINTOSH, F.R.S.
G. A. BOULENGER, Esq., F.R.S.
J. O. BORLEY, Esq., O.B.E.

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ALEXANDER BOWMAN, Esq., D.Sc.
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Capt. G. C. C. DAMANT, R.N., C.B.E.
Prof. J. STANLEY GARDINER, F.R.S.
RONALD D'O. GOOD, Esq.
Prof. E. S. GOODRICH, D.Sc., F.R.S.
Prof. A. C. HARDY.
Prof. A. V. HILL, F.R.S.
C. F. A. PANTIN, Esq.
C. TATE REGAN, Esq., F.R.S.
A. D. RITCHIE, Esq.
G. C. ROBSON, Esq.
J. T. SAUNDERS, Esq.
Prof. D. M. S. WATSON, F.R.S.

Chairman of Council.

Prof. E. W. MACBRIDE, D.Sc., F.R.S.

Hon. Treasurer.

GEORGE EVANS, Esq., 1 Wood Street, London, E.C.2.

Hon. Secretary.

E. J. ALLEN, Esq., D.Sc., F.R.S.,
The Laboratory, Citadel Hill, Plymouth.

The following Governors are also members of the Council :—

G. P. BIDDER, Esq., Sc.D.
E. T. BROWNE, Esq.
GEORGE EVANS, Esq.
H. G. MAURICE, Esq., C.B. (Ministry of Agriculture and Fisheries).
R. HOLLAND MARTIN, Esq., C.B. (Prime Warden of the Fishmongers' Company).
NIGEL O. WALKER, Esq. (Fishmongers' Company).
LOTHIAN D. NICHOLSON, Esq. (Fishmongers' Company).
Prof. G. C. BOURNE, D.Sc., F.R.S. (Oxford University).
J. GRAY, Esq., F.R.S. (Cambridge University).
Sir P. CHALMERS MITCHELL, KT., C.B.E., D.Sc., F.R.S. (British Association).
Prof. E. W. MACBRIDE, D.Sc., F.R.S. (Zoological Society).
Sir SIDNEY HARMER, K.B.E., F.R.S. (Royal Society).

List of Annual Subscriptions

Paid during the Year, 1st April, 1929, to 31st March, 1930.

	£	s.	d.
Dr. W. M. Aders	1	1	0
E. J. Allen, Esq., D.SC., F.R.S.	1	1	0
Aikawa, Hiroaki, Esq.	1	1	0
G. L. Alward, Esq.	1	1	0
Prof. J. H. Ashworth, D.SC., F.R.S. (1928 and 1929)	2	2	0
C. Amirthalingam, Esq. (1928 and 1929)	2	2	0
The Rt. Hon. Lord Askwith, K.C.B., D.C.L. (1928 and 1929)	2	2	0
Miss D. Atkins	1	1	0
G. R. de Beer, Esq.	1	1	0
Mrs. M. G. Bidder	1	1	0
Birkbeck College	1	1	0
H. Moss Blundell, Esq. (1927–1929)	3	3	0
Mrs. H. Moss Blundell (1928 and 1929)	2	2	0
L. A. Borradaile, Esq., D.SC. (1928 and 1929)	2	2	0
E. G. Boulenger, Esq. (1927–1929)	3	3	0
Col. Sir Henry Bowles, Bart. (1928 and 1929)	2	2	0
Dr. A. Bowman (1928 and 1929)	2	2	0
Dr. J. Borowik	1	1	0
Prof. A. E. Boycott, F.R.S.	1	1	0
Sir J. Rose Bradford, K.C.M.G., M.D., D.SC., F.R.S.	1	1	0
Brighton Public Library	1	1	0
H. H. Brindley, Esq. (1928 and 1929)	2	2	0
Miss E. M. Brown	1	1	0
Prof. F. Balfour Browne (1928 and 1929)	2	2	0
R. Brown, Esq.	1	1	0
Mrs. E. T. Browne (1928–1930)	3	3	0
R. H. Burne, Esq. (1928 and 1929)	2	2	0
R. R. Butler, Esq.	1	1	0
L. W. Byrne, Esq.	1	1	0
Dr. W. T. Calman, F.R.S. (1928 and 1929)	2	2	0
J. N. Carruthers, Esq.	1	1	0
Dr. A. H. Church, F.R.S. (1928 and 1929)	2	2	0
Dr. James Clark	1	1	0
R. S. Clark, Esq., D.SC. (1928–1930)	3	3	0
Carried forward	56	14	0

	£	s.	d.
Brought forward	56	14	0
Prof. F. J. Cole, D.SC., F.R.S.	1	1	0
J. S. Colman, Esq.	1	1	0
J. F. Coonan, Esq.	1	1	0
J. Omer Cooper, Esq. (1927–1929)	3	3	0
L. R. Crawshay, Esq.	1	1	0
Miss D. R. Crofts, D.SC.	1	1	0
N. Cuthbertson, Esq.	1	1	0
Prof. O. V. Darbishire	1	1	0
F. M. Davis, Esq. (1928 and 1929)	2	2	0
G. Despott, Esq. (1928–1930)	3	3	0
Director-General, Coastguard and Fisheries Service, Alexandria	1	1	0
F. A. Dixey, Esq., F.R.S.	1	1	0
C. C. Dobell, Esq., F.R.S.	1	1	0
Prof. J. C. Drummond (1928–1930)	3	3	0
F. Martin Duncan, Esq. (1928 and 1929)	2	2	0
Prof. J. S. Dunkerley, D.SC., PH.D.	1	1	0
Howard Dunn, Esq. (1928–1929)	2	2	0
V. C. Wynne Edwards, Esq.	1	1	0
P. Eggleton, Esq. (1928 and 1929)	2	2	0
Prof. C. Lovatt Evans, F.R.S.	1	1	0
George Evans, Esq.	1	1	0
G. P. Farran, Esq. (1928–1930)	3	3	0
Dr. R. A. Fisher, F.R.S.	1	1	0
The Fisheries Survey Committee, Capetown	1	1	0
Dr. Hussein Fawzy	1	1	0
Lt.-Col. T. Fetherstonhaugh, D.S.O. (1929 and 1930)	2	2	0
Dr. Ernest Foot	1	1	0
Dr. E. L. Fox (1928–1930)	3	3	0
Prof. H. Munro Fox (1928 and 1929)	2	2	0
Tadashi Fujita, Esq.	1	1	0
Miss E. A. Fraser, D.SC.	1	1	0
J. S. Gayner, Esq. (1929 and 1930)	2	2	0
S. G. Gibbons, Esq. (1927–1930)	4	4	0
Ronald D'Oyley Good, Esq.	1	1	0
Prof. E. S. Goodrich, F.R.S.	1	1	0
A. P. Graham, Esq. (1928 and 1929)	2	2	0
Dr. Robert W. Gray	1	1	0
J. R. Groome, Esq.	1	1	0
Dr. H. P. Hacker	1	1	0
Wilfred Hall, Esq.	1	1	0
Carried forward	120	15	0

	£	s.	d.
Brought forward	120	15	0
Prof. A. C. Hardy	1	1	0
C. R. Harington, Esq.	1	1	0
H. W. Harvey, Esq.	1	1	0
T. J. Hart, Esq. (1930 and 1931)	2	2	0
Dr. J. C. Hemmeter (1928 and 1929)	2	2	0
C. C. Hentschel, Esq. (1928–1930)	3	3	0
Prof. Sidney J. Hickson, D.SC., F.R.S. (1928–1930)	3	3	0
Prof. A. V. Hill, F.R.S.	1	1	0
Prof. J. P. Hill, F.R.S. (1928 and 1929)	2	2	0
Dr. W. T. Hillier	1	1	0
Prof. K. Hirasaka	1	1	0
Prof. Lancelot T. Hogben, D.SC. (1926 and 1927)	2	2	0
F. R. Horne, Esq.	1	1	0
Capt. G. C. L. Howell	1	1	0
O. D. Hunt, Esq.	1	1	0
Hull University College	1	1	0
J. J. Judge, Esq.	1	1	0
Stanley Kemp, Esq., D.SC.	1	1	0
Mrs. A. Redman King	1	1	0
P. Kirtisinghe, Esq.	1	1	0
Dr. G. Lapage	1	1	0
The Hon. Lionel Lindsay	1	1	0
A. G. Lowndes, Esq. (1928 and 1929)	2	2	0
J. R. Lumby, Esq.	1	1	0
Prof. D. L. Mackinnon, D.SC.	1	1	0
G. I. Mann, Esq. (1928 and 1929)	2	2	0
Prof. E. W. MacBride, F.R.S. (1928 and 1929)	2	2	0
Capt. W. N. McClean	1	1	0
D. J. Matthews, Esq. (1928 and 1929)	2	2	0
B. J. Marples, Esq.	1	1	0
Milford Haven Trawler Owners and Fish Salesmen's Association, Ltd. (1928 and 1929)	2	2	0
W. S. Millard, Esq.	1	1	0
Sir P. Chalmers Mitchell, Kt., C.B.E., D.SC., F.R.S.	1	1	0
C. C. Morley, Esq.	1	1	0
Dr. J. Mukerjii (1929 and 1930)	2	2	0
National Museum of Wales (1928 and 1929)	2	2	0
A. G. Nicholls, Esq.	1	1	0
Miss G. L. Naylor	1	1	0
Carried forward	176	8	0

	£	s.	d.
Brought forward	176	8	0
Charles Oldham, Esq.	1	1	0
G. W. Olive, Esq.	1	1	0
Prof. J. H. Orton, D.SC. (1928 and 1929)	2	2	0
R. Palmer, Esq.	1	1	0
G. W. Paget, Esq. (1928 and 1929)	2	2	0
The Hon. John H. Parker	1	1	0
C. W. Parsons, Esq.	1	1	0
Messrs. Pawlyn Bros.	1	1	0
T. A. Pawlyn, Esq.	1	1	0
Messrs. Peacock & Buchan, Ltd. (1929 and 1930)	2	2	0
F. T. K. Pentelow, Esq.	1	1	0
Prof. E. Percival	1	1	0
Port of Plymouth Incorporated Chamber of Commerce	1	1	0
Plymouth Public Library	1	1	0
Plymouth Proprietary Library (1928 and 1929)	2	2	0
Portsmouth Municipal College	1	1	0
W. P. Pycraft, Esq. (1928 and 1929)	2	2	0
C. Tate Regan, Esq., D.SC., F.R.S. (1927–1929)	3	3	0
H. G. Regnart, Esq.	1	1	0
E. A. Robins, Esq. (1928 and 1929)	2	2	0
G. C. Robson, Esq.	1	1	0
T. C. Roughley, Esq.	1	1	0
E. S. Russell, Esq., D.SC. (1928 and 1929)	2	2	0
F. S. Russell, Esq., D.S.C., D.F.C.	1	1	0
Capt. the Hon. Lionel St. Aubyn, M.V.O.	1	1	0
The Rt. Hon. Lord St. Levan, C.B., C.V.O.	1	1	0
R. E. Savage, Esq. (1928 and 1929)	2	2	0
J. T. Saunders, Esq.	1	1	0
Edgar Schuster, Esq., D.SC.	1	1	0
W. L. Sclater, Esq.	1	1	0
B. Sen, Esq.	1	1	0
Miss Lilian Sheldon	1	1	0
B. Webster Smith, Esq.	1	1	0
The Rt. Hon. the Earl of Stradbroke, C.B., C.V.O. (1928 and 1929)	2	2	0
States Committee for Fisheries, Guernsey (1928 and 1929)	2	2	0
A. C. Stephen, Esq. (1928 and 1929)	2	2	0
Mrs. N. S. Steven	1	1	0
E. J. Stream, Esq.	1	1	0
H. H. Sturch, Esq.	1	1	0
E. J. Tabor, Esq. (1928 and 1929)	2	2	0
Carried forward	233	2	0

	£	s.	d.
Brought forward	233	2	0
H. E. Tabor, Esq. (1928 and 1929)	2	2	0
J. M. Tabor, Esq. (1928 and 1929)	2	2	0
S. Takeda, Esq.	1	1	0
Prof. W. M. Tattersall	1	1	0
Sir Herbert F. Thompson	1	1	0
Harold Thompson, Esq., D.SC., (1928 and 1929)	2	2	0
Mrs. M. A. Thynne	1	1	0
Torquay Natural History Society (1928 and 1929)	2	2	0
Arthur Walton, Esq.	1	1	0
Alan H. Ware, Esq.	1	1	0
Prof. D. M. S. Watson, F.R.S.	1	1	0
W. H. Webster, Esq.	1	1	0
Mrs. F. J. Weldon	1	1	0
W. B. Woodrow, Esq. (1928 and 1929)	2	2	0
D. P. Wilson, Esq.	1	1	0
Dr. K. B. Williamson	1	1	0
R. S. Wimpenny, Esq. (1928 and 1929)	2	2	0
Ronald Winckworth, Esq.	1	1	0
C. M. Yonge, Esq., D.SC., PH.D. (1929 and 1930)	2	2	0
Total	£260	8	0

List of Composition Fees

Paid during the Year, 1st April, 1929, to 31st March, 1930.

	£	s.	d.
The Rt. Hon. Walter Guinness, D.S.O., M.P.	15	15	0
Miss E. A. T. Nicol	15	15	0
Leonard K. Elmhirst, Esq.	15	15	0
Geo. T. Atkinson, Esq.	15	15	0
Prof. W. Garstang, D.SC.	15	15	0
Prof. F. A. E. Crew, D.SC., M.D.	15	15	0
Total	£94	10	0

List of Donations to the General Fund

For the Year, 1st April, 1929, to 31st March, 1930.

	£	s.	d.
R. Hansford Worth, Esq.	5	0	0
Col. Sir Henry Bowles, Bart.	2	18	0
Dr. K. B. Williamson	2	2	0
Mrs. H. Roberts	1	0	0
Total	£11	0	0

THE MARINE BIOLOGICAL ASSOCIATION

Dr. *Statement of Receipts and Payments for the*

GENERAL

	£ s. d.	£ s. d.
To Balance from 31st March, 1929 :—		
Cash in hand	16 11 3	
Cash at Lloyds Bank £178 1 3		
Less Coutts & Co.—Overdraft 130 4 7	47 16 8	64 7 11
,, Grants :—		
Ministry of Agriculture and Fisheries Grant from Development Fund	11,152 10 5	
Fishmongers' Company	600 0 0	
British Association	50 0 0	
Royal Society (Gore Fund)	50 0 0	11,852 10 5
,, Subscriptions		260 8 0
,, Composition Fees		94 10 0
,, Donations		11 0 0
,, Sale of Specimens		1,384 16 1
,, ,, Fish (*less* Expenses)		55 11 6
,, ,, Nets, Gear, and Hydrographical Apparatus		720 5 3
,, Table Rent (including Cambridge University, £105 ; Oxford University, £52 10s. ; London University, £52 10s. ; Bristol University, £25 ; Leeds University, £10 10s. ; Imperial College of Science and Technology, £10 ; Trustees of the Ray Lankester Fund, £20)		410 7 0
,, Tank Room Receipts		487 0 3
,, Interest on Investments :—		
4% War Stock	3 2 8	
4% New Zealand Stock (Including Repayment of Income Tax)	26 5 6	29 8 2
,, Repayment £51 National Savings Certificates		69 8 6
,, Sale of Dr. M. V. Lebour's Book		6 4 10

The Association's Bankers held on its behalf :—
£410 14s. 8d. New Zealand 4%, 1943–63.
£237 17s. 11d. 4% War Stock, 1929–42 (Deed Stock).

£15,445 17 11

PLAICE EXPERIMENTS

	£ s. d.
To Grant from Ministry of Agriculture and Fisheries	225 0 0
,, General Fund	98 2 1
	£323 2 1

OF THE UNITED KINGDOM.

Year 1st April, 1929, to 31st March, 1930. **Cr.**

FUND.

	£	s.	d.	£	s.	d.
By Salaries :—						
Director	1,200	0	0			
Physiologist	910	0	0			
Naturalists	3,271	14	6			
Hydrographer	594	3	4	5,975	17	10
,, Laboratory Wages (including National Insurances)				1,899	18	4
,, Annual Upkeep of Library				636	7	1
,, Scientific Publications :—						
Journal, Vol. XVI, Nos. 1 and 2	756	11	4			
Less Sales	160	17	4	595	14	0
,, Annual Upkeep of Laboratories and Tank Rooms :—						
Buildings and Machinery	340	12	11			
Electricity, Gas, Coal, and Water	212	10	4			
Chemicals and Apparatus	505	8	5			
Rates, Taxes, and Insurance	96	17	5			
Travelling	121	8	2			
,, "Challenger" Society Meetings	29	5	2			
Stationery, Postages, Telephone, Carriage, and Sundries	446	18	7			
Purchase of Specimens	156	2	6	1,909	3	6
,, Annual Maintenance and Hire of Boats :—						
Wages (including Diet Allowance, National Insurance, and Casual Labour)	1,604	17	7			
Coal and Water	350	1	3			
Maintenance and Repairs, with Nets, Gear, and Apparatus	1,718	12	9			
Boat Hire and Collecting Expeditions	19	16	9			
Insurance	333	10	8	4,026	19	0
,, Interest on Bank Loan				9	0	5
,, Purchase of £91 15s. 11d. 4% War Stock 1929–42 (Investment of Composition Fees)	94	10	0			
,, Purchase of £67 12s 8d. 4% War Stock, 1929–42	69	8	6	163	18	6
,, Plaice Experiments Account :—						
Expenditure in Excess of Grant from Ministry of Agriculture and Fisheries				98	2	1
,, Balance, 31st March, 1930 :—						
Cash in hand	22	19	7			
Cash at Lloyds Bank £176 6 10						
Less Coutts & Co.—Overdraft 68 9 3	107	17	7	130	17	2
				£15,445	17	11

AT CAWSAND.

	£	s.	d.
By Salary of Mr. B. Dawes	225	0	0
,, Incidental Expenses	98	2	1
	£323	2	1

Examined and found correct,

3 *Frederick's Place,*
Old Jewry, London, E.C. 2.
25th *April*, 1930.

(Signed) N. E. Waterhouse, *Auditor.*
L. D. Nicholson } *Members of*
D. M. S. Watson } *Council.*

Marine Biological Association of the United Kingdom.

LIST

OF

Governors, Founders, and Members.

1st June, 1930.

* Member of Council. † Vice-President. ‡ President.

Ann. signifies that the Member is liable to an Annual Subscription of One Guinea.

C. signifies that he has paid a Composition Fee of Fifteen Guineas in lieu of Annual Subscription.

I.—Governors.

The British Association for the Advancement of Science, *Burlington House, W.* 1 ..... £940
The University of Oxford ..... £762 10*s.*
The University of Cambridge ..... £867 10*s.*
The Worshipful Company of Clothworkers, 41 *Mincing Lane, E.C.* 3 ..... £600
The Worshipful Company of Fishmongers, *London Bridge, E.C.* 4 ..... £20,955
The Zoological Society of London, *Regent's Park, N.W.* 8 ..... £500
The Royal Society, *Burlington House, Piccadilly, W.* 1..... £915
Bayly, Robert (the late) £600
Bayly, John (the late)..... £600
Thomasson, J. P. (the late) £970
*G. P. Bidder, Esq., Sc.D., *Cavendish Corner, Cambridge* £3008
*E. T. Browne, Esq., B.A., *Anglefield, Berkhamsted* £1235

II.—Founders.

1884 The Corporation of the City of London £210
1884 The Worshipful Company of Mercers, *Mercers' Hall, Cheapside, E.C.* 2 ..... £341 5*s.*
1884 The Worshipful Company of Goldsmiths, *Goldsmiths' Hall, E.C.* £100
1884 The Royal Microscopical Society, 20 *Hanover Square, W.* 1 £152 10*s.*
1884 Bulteel, Thos. (the late) £100
1884 Burdett-Coutts, W. L. A. Bartlett (the late) £100
1884 Crisp, Sir Frank, Bart. (the late) £100
1884 Daubeny, Captain Giles A. (the late) £100
1884 Eddy, J. Ray (the late) £100
1884 Gassiott, John P. (the late) £100
1884 Lankester, Sir E. Ray, K.C.B., F.R.S. (the late) £101
1884 The Rt. Hon. Lord Masham (the late) £100
1884 Moseley, Prof. H. N., F.R.S. (the late) £100
1884 The Rt. Hon. Lord Avebury, F.R.S. (the late) £100
1884 Poulton, Prof. Edward B., M.A., F.R.S., *Wykeham House, Oxford* £105
1884 Romanes, G. J., LL.D., F.R.S. (the late) £100
1884 Worthington, James (the late) £100
1885 Derby, the late Earl of £100
1887 Weldon, Prof. W. F. R., F.R.S. (the late) £100
1888 Bury, Henry, M.A., *The Gate House*, 17 *Alumdale Road, Bournemouth West* £100
1888 The Worshipful Company of Drapers, *Drapers' Hall, E.C.* £315
1889 The Worshipful Company of Grocers, *Poultry, E.C.* 2 ..... £120
1889 Thompson, Sir Henry, Bart. (the late) £110
1889 Revelstoke, The late Lord £100
1890 Riches, T. H., B.A., *Kitwells, Shenley, Herts* £430
1902 Gurney, Robert, *Bayworth Corner, Boars Hill, Oxford* ..... £107 1*s.*
1904 Shaw, J., K.C., *Adderbury House, Banbury, Oxfordshire* £113
1909 Harding, Colonel W. (the late) ..... £115 15*s.*
1910 Murray, Sir John, K.C.B., F.R.S. (the late) £100
1912 Swithinbank, H., F.R.S.E., F.R.G.S. (the late) £100
1913 Shearer, Dr. Cresswell, F.R.S., *Anatomy School, Cambridge* £100
1913 Heron-Allen, E., F.R.S., F.L.S., F.R.M.S., F.G.S., *Large Acres, Selsey Bill, Sussex* ..... £125 15*s.*
1920 McClean, Capt. W. N., 1 *Onslow Gardens, S.W.* 7 ..... £100
1920 Buckland of Bwlch, The Right Hon. Lord (the late) £105
1920 Llewellyn, Sir D. R. £105
1921 Harmer, F. W. (the late) £100
1923 Worth, R. H., 42 *George Street, Plymouth* ..... £120 15*s.*
1924 The MacFisheries, Ltd., 125 *Lower Thames Street, E.C.* 3 ..... £100

1924 Murray, Lady, 7 *Egerton Gardens, London, S.W.* 3..... £100
1925 The Institution of Civil Engineers, *Great George Street, Westminster*, S.W. 1 ..... £100
1927 Bidder, Miss Anna, *Cavendish Corner, Cambridge* £100

III.—Members.

1900 Aders, Dr. W. M., *Zanzibar, East Africa*..... £5 and Ann.
1928 Aikawa, Hiroaki, *Imperial Fisheries Institute, Fukagawa, Tokio, Japan* ..... Ann.
1923 Alexander, W. B., *Marine Biological Association, Cleveland Shipyard, Middlesbrough* £10
*1895 Allen, E. J., D.Sc., F.R.S., *The Laboratory, Citadel Hill, Plymouth* ..... £20 10s. and Ann.
1889 Alward, G. L., *Enfield Villa, Humberstone Avenue, New Waltham, Grimsby, Lincs.* ..... Ann.
1925 Amemiya, Dr. Ikusaku, *University of Tokyo (Agriculture and Fisheries Department), Tokyo, Japan* ..... Ann.
1927 Amirthalingam, C., *Department of Zoology, University College, Gower Street, W.C.* 1 ..... Ann.
1910 Ashworth, Prof. J. H., D.Sc., F.R.S., *Zoology Department, The University, Edinburgh* ..... Ann.
1921 Askwith, The Rt. Hon. Lord, K.C.B., D.C.L., 5 *Cadogan Gardens, London, S.W.* 3 .....£5 and Ann.
†1911 Astor, The Right Hon. the Viscount, 4 *St. James's Square, London, S.W.* 1 ..... £10 and *C.*
1910 Atkinson, G. T., *Fisheries Office, Esplanade, Lowestoft, Suffolk*... *C.*
1929 Atkins, Miss D., *Woodlands, Eridge Road, Crowborough, Sussex*... Ann.

1920 Baker, J. R., *New College, Oxford*, and *The Dell, Malvern Wells* £1 and *C.*
*1928 Barcroft, Prof. J., F.R.S., *Glenveagh, Grange Road, Cambridge*... Ann.
1923 Barnard, K. H., *South African Museum, Cape Town, South Africa* £10
1923 Barnard, T. T., *King's College, Cambridge* £11
1929 Bayliss, L. E., *St. Cuthbert's, West Heath Road, London, N.W.* 3 £10 and *C.*
1921 Bazeley, W. J., *The Cliff, Penzance, Cornwall*..... Ann.
1885 Beck, Conrad, C.B.E., 34 *Upper Addison Gardens, London, W.* 14 *C.*
†1907 Bedford, His Grace the Duke of, K.G., *Endsleigh, Tavistock* £20 and *C.*
1928 Beer, G. R. de, 4 *Holywell, Oxford* ..... Ann.
1926 Bělehrádek, J., M.D., *Docent of General Biology, Masaryk University (Medical Faculty), Brno, Czechoslovakia*..... Ann.

1925 Berrill, N. J., *McGill University, Montreal, Canada* ..... Ann.
1903 Bidder, Colonel H. F., *Ravensbury Manor, Mitcham, Surrey*..... Ann.
1910 Bidder, Mrs. M. G., *Cavendish Corner, Cambridge* ..... Ann.
1925 Birkbeck College, *Bream's Buildings, Fetter Lane, London, E.C.* 4 Ann.
1910 Bloomer, H. H., "*Longdown,*" *Sunnydale Road, Swanage, Dorset* ..... Ann.
1921 Blundell, H. Moss, *Ministry of Agriculture and Fisheries, 43 Parliament Street, London, S.W.* 1 ..... Ann.
1922 Blundell, Mrs. H. Moss, *Callipers Hall, Chipperfield, King's Langley, Herts*..... Ann.
†1910 Borley, J. O., O.B.E., M.A., 5 *Queen Anne's Chambers, Dean Farrar Street, S.W.* 1..... £1 1*s.* and Ann.
1928 Borowick, Dr. J., *National Scientific Institute of Agriculture, Zacisze* 8, *Bydgoszcz, Poland* ..... Ann.
1918 Borradaile, L. A., Sc.D., *Selwyn College, Cambridge* £1 1*s.* and Ann.
1923 Boulenger, E. G., *Zoological Society, Regent's Park, London, N.W.* 8..... Ann.
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